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Limacosphaera, an Unusual Mesogastropod (Lamellariidae) Larva of the Weddell Sea (Antarctica)

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ABSTRACT

Marseniopsis conica Smith, 1915 and *M. mollis* (Smith, 1902) have planktotrophic larvae that are unique among gastropods. They cover the larval shell with a lacunous muscular mantle that can change its volume by interaction of body fluid and muscle activity. This limacosphaera larva is found in Antarctic waters and represents the most complex larval strategy within the "echinospira-group". Notes on the biology and anatomy, including histology, of this larva are presented.

Key words: Lamellariidae, *Marseniopsis*, larvae, Antarctica.

INTRODUCTION

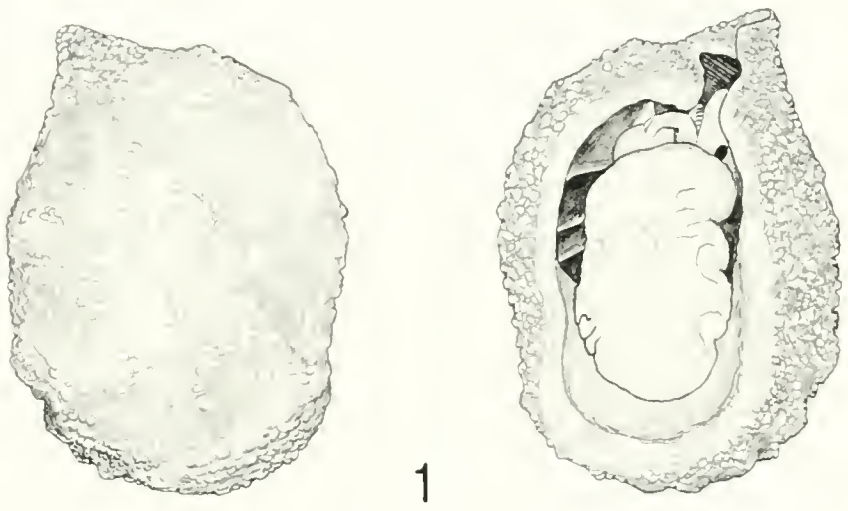
The majority of benthic invertebrates of high-Antarctic seas brood their young or provide postspawning parental care rather than produce free-living larvae (Mileikovsky, 1971; Picken, 1980). True planktotrophic pelagic larvae are extremely rare in the 200 to 600 m deep high-Antarctic shelf areas.

Plankton samples taken by the R/V POLARSTERN in the eastern Weddell Sea during several late winter to late summer cruises yielded only two meropelagic larvae of benthic gastropods (Piatowski, 1987; Boysen-Ennen, 1987). Both of these larval types were regularly found. One of these is *Capulus subcompressus* Pelseneer, 1903, which had first been observed by Pelseneer (1903) and is described in detail by Bandel and Hain (in preparation). The second meropelagic larvae was first observed by Simroth (1914) in material from the Davis Sea. Simroth noted anatomical similarity to a planktonic gastropod from the deep sea areas of the Indian Ocean, which he described earlier as *Limacosphaera macdonaldi* (Simroth, 1908).

This animal is a spherical, transparent, voluminous gastropod with two openings: one to allow head and foot to come out of the shell and the other situated on the opposite side of the sphere (Simroth, 1908, 1914). Simroth called the muscular mantle covering the larval shell the deutoconcha of the limacosphaera. The posterior pore, which he (1908) called the shell tunnel (Schalengang), connects the sea water with a cavity surrounding much of the thin organic shell. Simroth (1914) also suggested the presence of glandular cells and muscle fibers in the voluminous deutoconcha that surrounds the shell. He noticed that the Antarctic forms represented larvae rather than adult gastropods as he had originally assumed when describing *Limacosphaera* as a new genus of pelagic gastropods (Pteropoda). Simroth (1914) correctly placed these larvae into the ontogeny of members of the "echinospira-group" in the genus *Marseniopsis*. The term limacosphaera was retained, now to describe a very peculiar and characteristic larva.

Simroth (1908, 1914) considered that the limacosphaera swam with the aid of their large velum. Another mode of swimming, mainly by hydrostatic effects, was considered the likely mode of propulsion in the water column by Jevdonin and Minichev (1975).

These authors observed developing spawn of *Marseniopsis conica* and found that the mantle of the embryo envelops the shell prior to hatching from an egg mass found in excavations of tunicate surfaces. Jevdonin and Minichev (1975) also noted that the mantle did not fuse completely but left an open shell pore. They seem not



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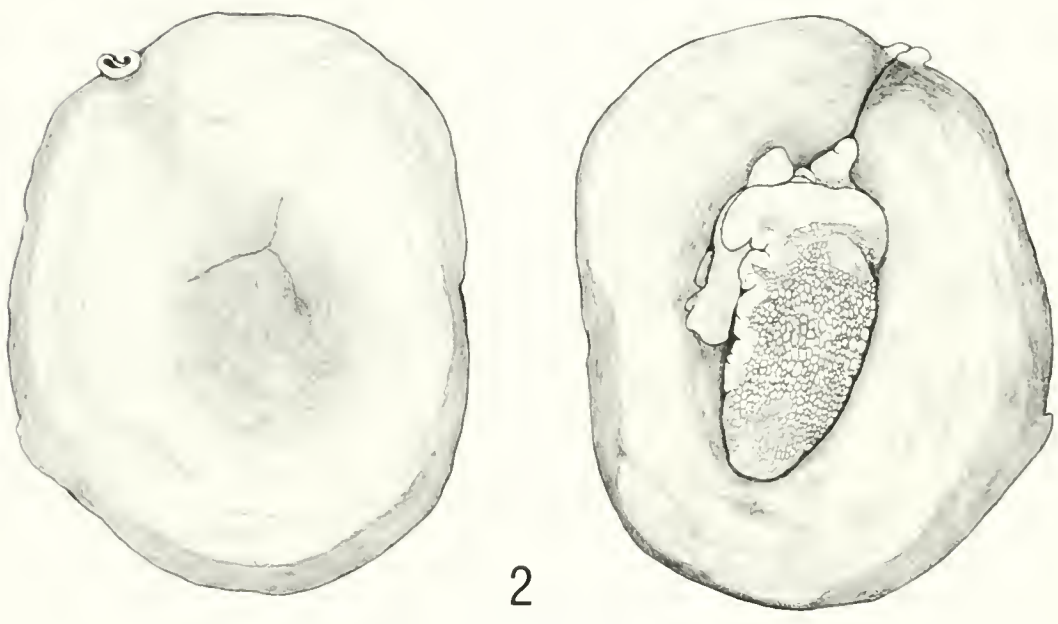

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Figures 1, 2. Adult animals of **1.** *Marseniopsis conica* Smith, 1915, and **2.** *M. mollis* (Smith, 1902). Dorsal views on left, showing mantles that are fused above the shell and cannot be retracted. Ventral views on right, show foot, parts of the head. All illustrations drawn from fixed animals. Scale bar = 5 mm for figure 1, 10 mm for figure 2.

to have been aware of the earlier descriptions of these larvae by Simroth (1908, 1914). Jevdonin and Minichev (1975) suggested that larvae with a size of about 20 mm in diameter were nearly ready to metamorphose. Their descriptions suggest that their observations had been carried out on preserved material and they most probably did not see living larvae or embryos.

We provide a new description of the histology of these larvae integrated with observations on the living forms and their metamorphosis.

MATERIALS AND METHODS

During the cruises POLARSIRKEL 80/81, POLARSTERN ANT I, ANT III/3, ANT V/3 and ANT VII/4 larvae of the limacosphaera type were caught at about 100 stations in

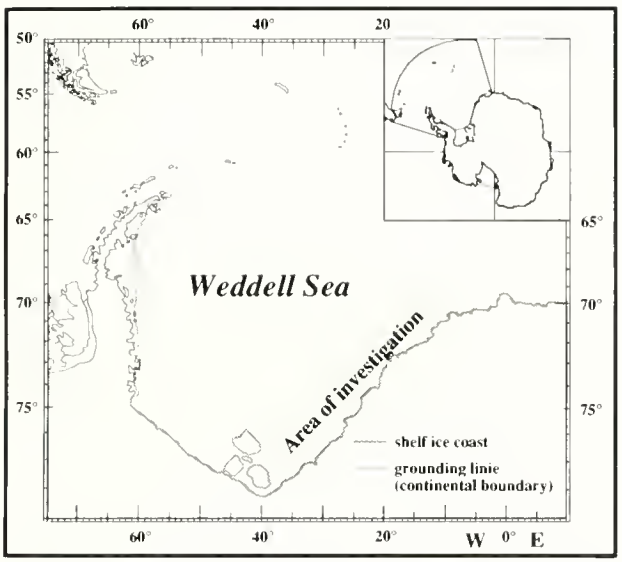


Figure 3. Map indicating location of the Wedell Sea and the area where the larvae of *Marseniopsis* were caught.

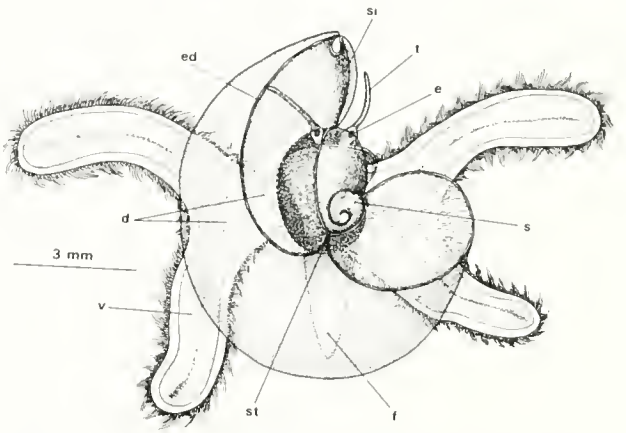


Figure 4. Larva of *Marseniopsis cf. mollis*. Schematic drawing from several photographs of living specimens. One quarter of the shell-covering tissue (deutoconcha) is removed. d, deutoconcha; e, eye; ed, epidermis; f, foot; s, shell; si, siphon; st, apical tube; t, tentacle; v, velum.

neritic waters above continental shelf areas of the eastern Weddell Sea (figure 3). Samples were taken with various plankton gears (mesh sizes of 0.335–4.5 mm) in upper water layers (300–0 m) and preserved in buffered formalin.

Six larvae were kept alive for six weeks during the expedition PS ANT V/3. During this period they were fed two times with a diatom suspension. Only one of the larvae survived and metamorphosed four weeks after capture (November 1986). It was fixed in 70% ethanol.

During the expedition PS ANT VII/4 (January to March 1989) 42 living limacosphaera from RMT samples were photographed for size measurements and transfered individually to small plastic aquaria (running water system, temperature adjusted to 0 °C). The larvae were fed once a week with a suspension of Antarctic diatoms. After 8 and 13 months the photographic measurements of larvae or juveniles were repeated.

The larval shell, the thick, whitish to semitransparent tissue covering it (deutoconcha), and the juvenile shell were studied on 10 critical-point dried specimens using a SEM.

In May 1989, six living larvae were fixed for histological studies in 4% seawater-formalin or 2.5% seawater-glutaraldehyde. One limacosphaera fixed in formalin was dehydrated using isopropanol. It was then treated with benzylbenzoate, embedded in paraplast, serially sectioned (7 μm) and stained with Helioechtrubin BBL/Acidgreen 5/Acidorange 10 after Halmi (Adam & Czihak, 1964).

To detect lipids whole larvae without the deutoconcha as well as parts of the deutoconcha were treated using the oil-red-method (Romeis, 1968). These samples were embedded in glycerin and examined with a light microscope.

Another limacosphaera fixed in glutaraldehyde was osmicated in 1% osmium tetroxide, dehydrated in acetone and embedded in Spurr's fluid. Sections were cut at *ca.* 80 nm to 1 μm using an ultramicrotome (Reichert). The 80 nm sections were stained with uranyl acetate and lead citrate, then examined and photographed using a TEM (Zeiss). The 1 μm sections were stained with Toluidine Blue and Pyronin and examined with a light microscope.

Voucher material is deposited at the Zoological Institute and Museum (University of Hamburg) (cat. no. M 885).

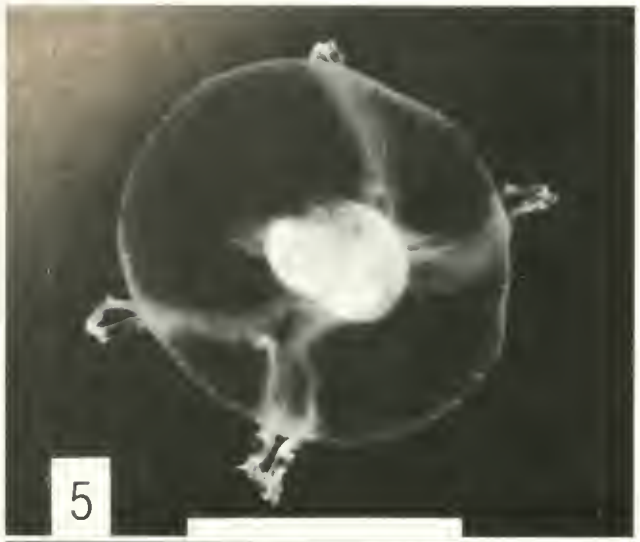
RESULTS

The Living Larva

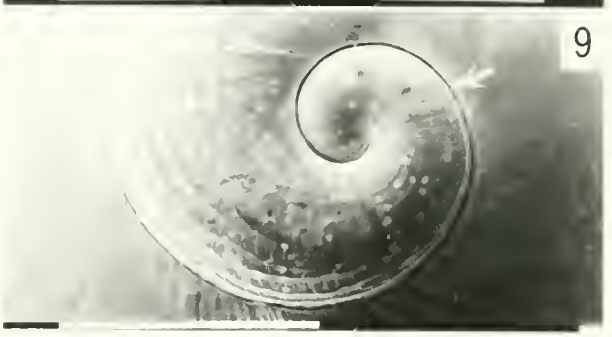
Description: The shape of the limacosphaera (figures 4–6) is globular with an overall diameter ranging from 1.8 to 20 mm. The actual larval shell is covered by the deutoconcha. Some of the larvae have granular deposits in the outer layer of the deutoconcha. On the ventral side of the larva (figure 6) there is a slit-like opening for the foot and the four large velar lobes. This opening is extended anteriorly by a siphon-like, semicircular groove. A second, small, tunnel-like excavation extends from the apical region of the shell to the surface of the deutoconcha. Observations on living larvae sorted from plankton samples show that both openings can be closed and that the deutoconcha produces much hyaline mucus.

During metamorphosis the shell is still barely calcified (figure 7), becoming solidly calcified right after metamorphosis (figure 8). The larval shell reaches 2.3 whorls with fine spiral threads on the first 1.5 whorls. Earliest growth lines are visible after 0.8 whorls (figure 9 arrow). In well fed larvae, the greenish visceral mass can be seen through the shell and the deutoconcha.

All studied larvae had a well developed foot. The eyes are at the base of the tentacles. In contrast to Simroth's original description of *Limacosphaera macdonaldi* from



Figures 5, 6. Living larvae of *Marseniopsis cf. mollis*. **5.** Dorsal view. **6.** Ventral view, with foot, velum, tentacles and eyes visible. Scale bars = 5 mm for both photographs.



Figures 7–9. Shell of *Marseniopsis cf. mollis*. **7.** During metamorphosis, the shell is barely calcified and therefore, flexible. **8.** After metamorphosis, shell solidly calcified and has reached 2.4 whorls. **9.** Same specimen as in fig. 8. First growth lines (arrow) are visible at 0.7 whorls of the shell. The spiral threads end at 1.4 whorls. Scale bars = 1 mm in all photographs.

the tropics, the operculum is absent in the Antarctic specimens.

Biology

Deposition of egg capsules in the tests of compound ascidians is known for temperate lamellarian species (Fretter & Graham, 1962). Antarctic species have the same spawning habit (Jevdonin & Minichev, 1975; P. Dayton, personal communication). One compound ascidian with approximately 20 egg capsules was obtained in February 1989. Although maintained in an aquarium, the eggs failed to develop.

Larval size, as well as the time and location of sampling, indicates that hatching of larvae occurs from late winter to austral summer in the shelf areas of the eastern Weddell Sea.

The smallest larvae found have a diameter of 1.8 mm. We suggest that this size is reached shortly after the larvae have hatched and risen from the bottom. Aquarium observations indicate that the larvae rise by buoyancy. The large velar lobes are not used or have only secondary function. The buoyancy control mechanism is unknown.

In the northern shelf areas of the Weddell Sea the amount of food (0.07 μg chlorophyll-a/liter) is more

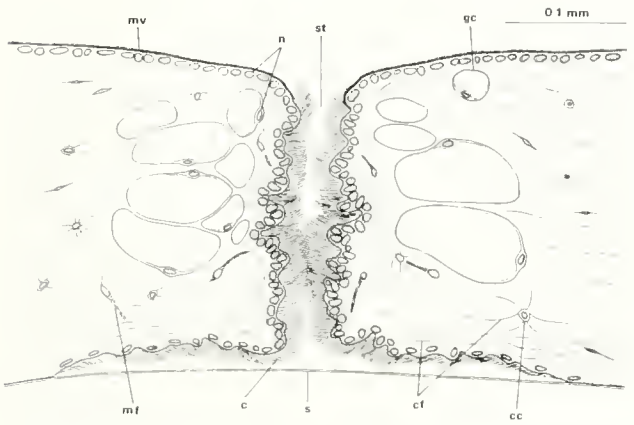


Figure 10. Schematic drawing of the apical tube (shell tunnel) of *Marseniopsis cf. mollis*. c, cilia, cc, collagenous cell, cf, collagen fibers; gc, gland cell; mf, muscular fibers; mv, microvilli; n, nuclei; s, shell; st, apical tube

limited even during phytoplankton blooms. In open waters or polynyas (ice free areas), the phytoplankton concentration barely reaches 1.5 μg chl·a/liter. It is suspected that growth of larvae in these areas takes a much longer time.

The total lipid content of larvae caught in February (end of austral summer) is low (3.5% dry weight) in comparison to other planktonic organisms. Seventy percent of these lipids are triacylglycerols (Hagen, 1988).

Although fed only twice, one limacosphaera caught in October 1986 metamorphosed four weeks later. During PS ANT VII/4 small larvae with a diameter of 3.9 mm began to metamorphose in the aquaria after 10 to 24 hours, while specimens of 10 mm diameter remained in the larval stage for up to 8 weeks. One specimen caught in the end of February 1989 was still in the larval stage when it died in August 1990.

Predatory pressure on the larvae seems to be very low. The shell-covering tissue of juveniles and adults is known to produce acidic secretions.

HISTOLOGY

Observations with Light Microscope

The deutoconcha of the limacosphaera consists of tissue that is composed of an outer epidermis, a central, cavernous connective tissue, and an inner epidermis covering the shell.

The outer epidermis is composed of a single layer of cells with flattened nuclei and immersed, large, light, glandular cells with a single nucleus. Below it is a voluminous, spacious connective tissue, consisting of collagenous and muscular fibers with few cells suspended in it. The inner epidermis is a single layer of cells supported by connective tissue and musele fibers. These cells are stretched in length, and their nuclei are even more flattened than those of the outer epidermis.

The deutoconcha of the limacosphaera is connected to the inner mantle of the apertural region of the shell by an especially strong museular bridge of tissue. The outer mantle rests on the shell near the aperture and forms the connection to the inner mantle covering the visceral mass and the pallial cavity. Outer and inner mantle are "divided" from each other by the periostracal gland zone characterized by the presence of many nuclei.

On the apical side of the deutoconcha the external mantle is pierced by a tube-like canal (figure 10, st) connecting sea water and shell surface. This canal is lined with a rugged, ciliated epithelium (figure 10, c) that continues along the inner mantle for about 0.4 mm, to form a small cavity between shell and mantle (figure 10). The tissue below the ciliated epithelium of the canal contains an agglomeration of large light epithelial glandular cells.

The inner side of the deutoconcha connects to the organic shell that is composed of a double-layered periostracum. This shell in its apical portion is filled with the visceral mass containing the large digestive gland. Its diverticula consist of large endodermal cells with basal nuclei and small cavities. The apical portion of the digestive gland is glandular and contains three different types of stored substances. The most basal portion contains proteins, somewhat above lie a large number of spherical bodies. Scale-like storage material that is weakly acidophilous is suspended between these.

The spherical bodies (6–19 μm in diameter) are lipids (analysed by oil-red method). The spheres of lipids were arranged like strings of pearls of different length throughout the entire digestive gland of a larva caught in February 1989 during the phytoplankton bloom.

The outer surface of the deutoconcha was also tested for the presence of lipids, but was found to lack them. This test was repeated on another larva that had been caught prior to the beginning of the phytoplankton bloom (mid-November 1986). It lacked lipids in either the mantle or the digestive gland.

Of the other organs of the larva, the nerve ring proved to be quite large. The eyes were well-developed, with lens-like light collectors. The foot is intensely ciliated, almost to the same degree as the large velum. The radula is well developed and functional.

Observations with Electron Microscope

The epidermis of the deutoconcha (figure 11) is covered by a 2 μm high rim of microvilli. These microvilli are differentiated into a narrow basal portion with many filaments and a light, partly bubble-like expanded upper portion.

These "bubbles" are secretory vesicles, usually linearly arranged and attaining 2–4 times the width of the microvilli. They are produced by glandular cells at the base of the rim of microvilli and are secreted at the outside of the rim. "Bubbles" open up at the outside of the rim as could be seen in some sections.

The surface of the rim of microvilli is covered with fine fibrillar material containing small dark granules.

Between microvilli, larger vesicles with a small internal membrane are often present. Some larger vesicles are as high as the microvilli and are connected to the glandular vesicles of the epidermis.

The epithelium of the deutoconcha consists of a single layer of flattened cells resting on a distinct basal membrane. The cells are up to 10 μm in size, and are connected to each other by apical contact zones. Cell boundaries are strongly folded and intercalated.

Some nuclei are strongly heterochromatic, others are large, less densely packed and of irregular shape. All cells hold large, light vesicles often containing membranous extensions. These vesicles form a loosely connected system that is in contact with the vesicles extruded into the rim of microvilli. Newly extruded vesicles hold dense granules.

A voluminous connective tissue is present below the epidermis and fills the space between inner and outer layer of the deutoconcha. Within a homogeneous basal substance, individual, transversally striped fibers of collagen connect the basal membrane of cells within the tissue to the epidermis.

Large cavities lie within the connective tissue near the epidermis. These cavities are lined with a thin, conspicuously foamy cellular layer resting on a basal membrane. The nuclei are flattened and elongated.

Nerves, consisting of several axones within a glial cell, and smooth muscular fibers with connections to the collagen fibers are distributed within the connective tissue.

The intermediate layer between outer and inner epithelia (gelatinous layer, Simroth, 1908) is shown to contain a network of collagenous fibers connected to muscle and epithelial cells. This layer functions together with interconnected blood lacunae as a hydroskeleton that can change the outline, shape and width of the limacosphaera.

The apical tube (figures 4, 10, st) of the deutoconcha is ciliated, in contrast to the remaining surface of the mantle. This ciliation continues into the small cavity at the proximal end of tube above the shell. This cavity is less extensive than assumed by Simroth (1908) and does not surround the entire shell surface.

Simroth (1908) noted a folded surface of the shell, which is an artifact of preservation.

A rim of microvilli on a unilayered epithelium surrounding a structured connective tissue represents a large surface for resorption as well as for secretion by many glandular cells that come together in canals opening into pores. The type of secretion produced by these glands is unknown. The secretion expelled between the microvilli probably represent neutral mucus material.

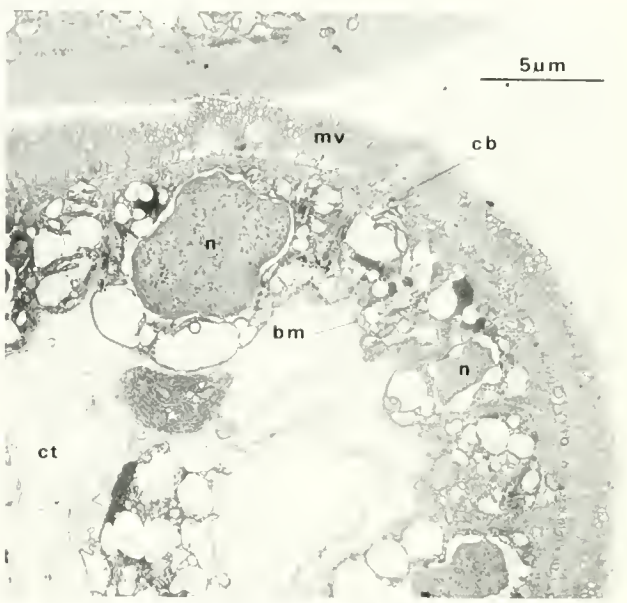


Figure 11. Transmission Electron Micrograph of the deutoconcha epidermis of *Marseniopsis cf. mollis*. bm, basal membrane; cb, cell boundary; ct, connective tissue; mv, microvilli; n, nucleus.

DISCUSSION

The larvae metamorphosed into juveniles that had either a smooth surface or a tuberculated body surface. Both juvenile forms were analysed by gel-electrophoresis (1D-DISK-SDS-PAGE) at the Alfred-Wegener-Institut (Dr. T. Stadler). The results were compared to gel-electrophoresis (same method) analyses of adult *Marseniopsis conica* and *Marseniopsis mollis*. Differences in the data indicate that the predominantly smooth juveniles represent *M. mollis* and the tuberculated ones *M. conica*. Thus it can be concluded that both species have very similar larvae. It was not possible to section and electrophoretically analyse the same individual.

The course of a limacosphaera's development depends on a variety of factors, including currents in the upper water layers, melting of sea ice, and patchyness of phytoplankton production. Larval survival in captivity for 1.5 years indicates that a limacosphaera could remain in the plankton for over a year if conditions were not favorable for metamorphosis.

Analyses of lipid content suggest that larvae either use most food-energy for growth or they store energy in form of other biochemical metabolites (*e.g.*, proteins). The vertical distribution and the stomach contents of larvae caught during mid-October at 72°S indicate that they feed under the sea ice where the phytoplankton concentration (0.07 μg chl·a/liter) was seven times larger than in deeper water (Scharek, personal communication). Due to the southwesterly water currents near the surface, the majority of larvae will be transported to southern parts of the study area, where very high phytoplankton concentrations (50–150 μg chl·a/liter) were measured directly under the sea ice in October 1989. By utilization of this enormous food resource, larvae living in that area could grow very rapidly. Due to the fact that the macrozoobenthos community of the southern Weddell Sea is totally different from that of the eastern Weddell Sea (Voss, 1988) and therefore not suitable for survival of benthic stages of *Marseniopsis*, there must be a way of

returning pelagic stages (metamorphosing larvae, juveniles or adults) back to the hatching grounds. This may be accomplished by counter-currents running near the bottom.

Piatkowski (1987) and Boysen-Ennen (1987) reported the absence of larvae in the oceanic domain between the tip of the Antarctic peninsula and the north-eastern part of the Weddell Sea. *Marseniopsis* populations of the peninsula are likely zoogeographically separated from populations in the eastern Weddell Sea. Nevertheless some of the larvae could be transported by eastward wind drift of surface water layers near the ice edge from eastern-Antarctica to the Weddell Sea. Between February and March 1983, the mean abundance of larvae in the eastern Weddell Sea was 24 specimens per 1,000 m^3 (Boysen-Ennen, 1987), with maximum densities of 65 larvae per 1,000 m^3 in the southern part of the study area (Piatkowski, 1987). Most larvae were found in water layers of 200 to 50 m (63%) and 50 to 0 m (35%), only 2% were reported from 300 to 200 m depth (Boysen-Ennen, 1987). The major function of the deutoconcha is that of a buoyancy organ. Altering the volume of the outer mantle may vary the speed of sinking of the limacosphaera. According to Stoke's formula (Tiemann & Betz, 1979) this speed depends on the specific weight, which again is a function of the diameter of the limacosphaera. Histological analyses of the limacosphaera showed that the deutoconcha contains very little organic material and is thus very close to the density of sea water. The deutoconcha can enlarge the diameter and thus the volume of the larva without decreasing its weight in the water. A general calculation indicated that the voluminous outer mantle of the limacosphaera decreases the speed of its sinking to about one half of what it would be without such a cover around the shell.

The ability to float was observed in aquaria for all developmental stages. Even large adult specimens could float near the bottom after disturbance (diving observations at the Antarctic peninsula, W. Wägele, personal communication).

The function of the deutoconcha's apical tube and cavity is still unknown. It is evident that water can be pumped into the cavity and expelled out by ciliary currents as well as by muscular movements of the deutoconcha. It is also evident that glands can secrete substances into the lumen of tube and cavity.

Histological examination of the limacosphaera for the most part confirms the observations of Simroth (1908, 1914). His assumption that muscular cells are present within the deutoconcha is substantiated.

The prolific mucus secretion of the entire deutoconcha, as well as its large size may serve as defensive mechanisms against carnivorous planktonic groups like copepods or krill.

The shell size of hatching larvae can only be interpreted from the embryonic and the larval shell (figure 8). There are two possibilities. The normal case would be that the embryo hatches shortly after the beginning of growth lines (the mantle becomes free from the shell) (figure 9, arrow). This happens after 0.8 whorls and a diameter of the shell of 0.65 mm.

The second possibility is that the embryo does not hatch before reaching 1.4 whorls (with spiral threads). The shell then has a diameter of 1.5 mm. To reach this size the embryo would have to feed on extra yolk.

It is proposed that the embryo hatches when the shell has reached 1.4 whorls. At this time the spiral threads disappear. This is probably the consequence of the mantle fusing above the shell. There is no difference in sculpture between the subsequent part of the larval shell and the teleoconch of the investigated species of *Marseniopsis*.

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The Reproductive Anatomy of *Philomycus sellatus* Hubricht, 1972 and *Philomycus virginicus* Hubricht, 1953 (Gastropoda: Philomycidae)

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ABSTRACT

Specimens of *Philomycus sellatus* and *P. virginicus* were collected at or near their type localities. Their reproductive anatomy is described and compared with that of other species of *Philomycus*. The penial anatomy of *P. sellatus* is unique in having two constrictions in the penial wall. *P. virginicus* is distinguished by a circular pustulose ridge that separates the distal penis from its atrial opening.

Key Words: Mollusca, Gastropoda, landsnail, slug, Philomycidae, *Philomycus*, reproductive anatomy

INTRODUCTION

All species of the terrestrial slug family Philomycidae have a mantle that covers the entire body of the slug. Three genera of this family, *Philomycus*, *Pallifera*, and *Megapallifera*, occur in the United States, with most species being limited to the eastern and south-central areas of the country. Few original descriptions provide anatomical data. Neither the description of *Philomycus virginicus* Hubricht, 1953 nor of *P. sellatus* Hubricht, 1972 discusses or figures any part of the reproductive anatomy. Based upon the mantle pattern, Hubricht (1972) compared *Philomycus sellatus* to *P. carolinianus* (Bosc, 1802), but made no comparisons between *P. virginicus* and other species of *Philomycus*. References to the reproductive anatomy of *P. virginicus* are limited to two articles by Branson (1968, 1969) that compared *P. virginicus* with *P. bisdosus* Branson, 1968. Neither contain figures or measurements. The reproductive anatomy of *P. sellatus* has not previously been studied.

The goals of the present study were to describe the anatomy of the reproductive systems of *Philomycus virginicus* and *P. sellatus*, and to compare them with those of other species of *Philomycus*.

METHODS AND MATERIALS

Specimens of *Philomycus virginicus* were collected on 19 May 1989 near milepost 47 north of Skyline Drive, Shenandoah National Park, Madison County, Virginia, under the loose bark of logs and dead trees, elevation approximately 1110 meters. This station was approximately 0.5 kilometers east of the type locality for this species. Specimens of *P. sellatus* were collected on 17 May 1989 from its type locality (2.7 kilometers northeast of Princeton, along Highway 65, Jackson County, Alabama) in beetle galleries in rotten logs, elevation approximately 215 meters. For comparative purposes, the following species were also examined: *P. carolinianus* collected in Berkeley County, South Carolina approximately 25 kilometers from Charleston, the designated type locality (Pilsbry, 1948:754) on 22 June 1988. *P. bisdosus* collected from Breaks Interstate Park, Dickenson County, Virginia (the type locality) on 22 May 1987. *P. flexuolaris* collected from Breaks Interstate Park, Dickenson County, Virginia on 22 May 1987, and *P. togatus* collected near Riceville, Pittsylvania County, Virginia on 20 May 1987.

External characteristics of the specimens were compared with the original species descriptions to ensure correct identification. All specimens were drowned in distilled water and dissected immediately. The reproductive systems were removed and the atrium and penis opened to examine their internal anatomy. Subsequently all material was preserved in 70% ethanol. Drownings and dissections were conducted during the month of June in each year to reduce any differences that may be attributable to the stage of the life cycle. The specimens were maintained in terraria for approximately two weeks prior to dissection.

Each complete reproductive system was spread out in a petri dish and then projected, via an overhead projector, and traced. The penial figures are tracings of photographic slides of the opened organs. Voucher specimens have been deposited in the Academy of Natural Sciences, Philadelphia (ANSP A13326 for *Philomycus bisdosus*, ANSP A13327 for *P. virginicus*, ANSP A13328 for *P. sellatus*, and ANSP A13329 for *P. carolinianus*).

RESULTS

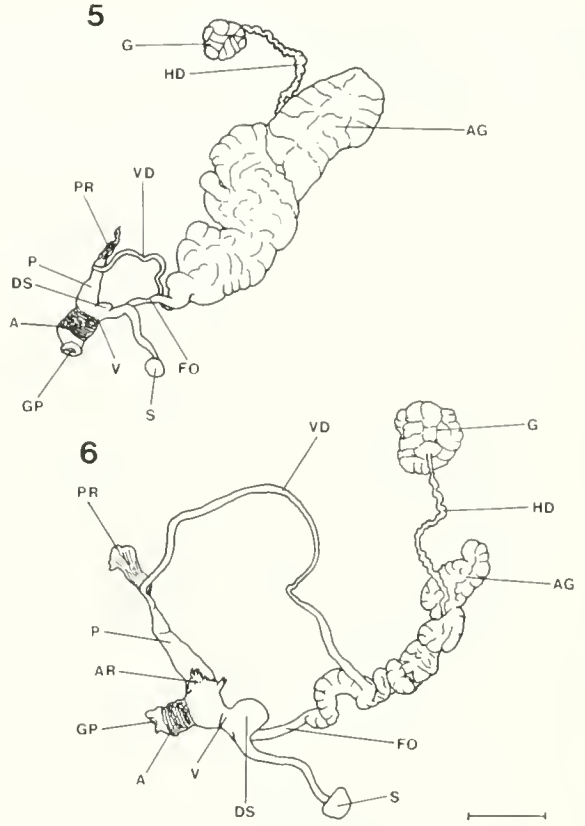
Four adult specimens each of *Philomycus sellatus* and of *P. virginicus* were collected and used in the study.

Figures 1–4. Mantle patterns of living slugs. **1, 2.** *Philomycus virginicus* **3, 4.** *Philomycus sellatus*. Scale bar = 20 mm.

External characteristics of all four specimens of each species (figures 1–4) agreed with their type descriptions. The gross reproductive anatomy was similar for all specimens of a species. Measurements of selected reproductive organs are shown in Table 1.

Genitalia of *Philomycus sellatus* Hubricht, 1972 (figures 6, 8)

Atrium glandular on distal half of outer surface, length approximately 60% penial length. Vagina length approximately 10% of penis. Spermathecal duct approximately same diameter as free oviduct, length nearly twice that of free oviduct, slight taper toward spermatheca. Spermatheca round. Dart sac (with dart) larger than spermatheca. Penis diameter at proximal end nearly equal to atrial diameter, gradual taper to diameter of vas deferens at distal end; penial sheath covers approximately

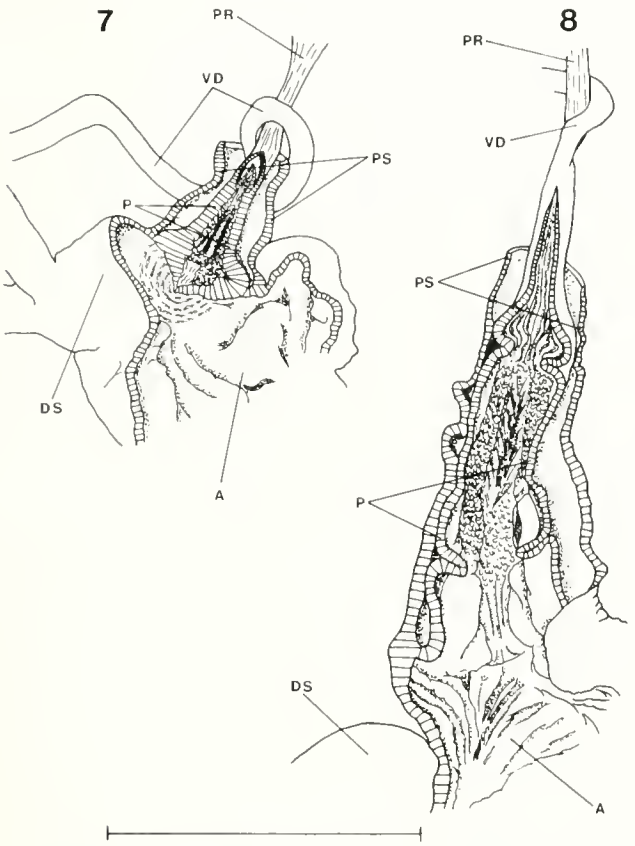


Figures 5, 6. Genitalia **5.** *Philomycus virginicus*. **6.** *Philomycus sellatus*. Scale bar = 10 mm. A: atrium, AG: albumen gland, AR: accessory retractor, DS: dart sac, FO: free oviduct, G: gonad, GP: genital pore, HD: hermaphroditic duct, P: penis, PR: penial retractor, S: spermatheca, V: vagina, VD: vas deferens.

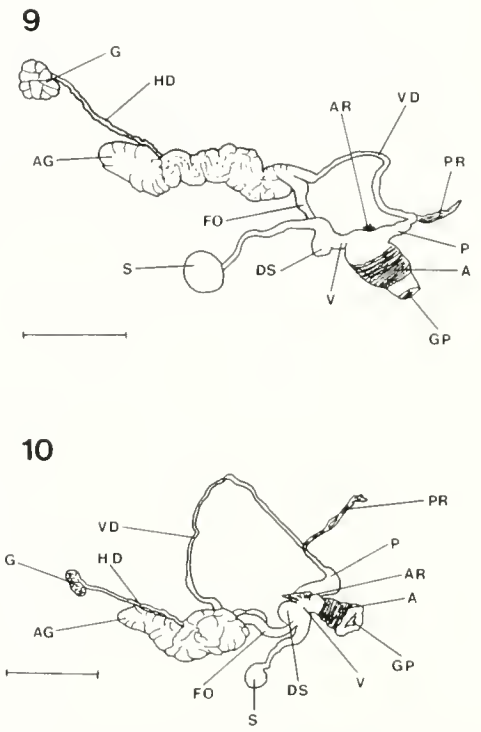
90% of penis. Internally, distal third of penis with several thin low folds, separated from remainder of penis by constriction in penial wall; middle third with 3–4 large pustulose ridges; proximal third with several thin nonpustulose folds, separated from middle third by constriction in penial wall. Vas deferens enters distal end of penis, length approximately four times that of penis; diameter of middle third half that of ends. Penial retractor muscle maximum width 2–3 times diameter of distal end of penis, length 40% of penis. Accessory retractor muscle present, located on outer wall of atrium near its junction with penis.

Genitalia of *Philomycus virginicus* Hubricht, 1953 (figures 5, 7)

Atrium length approximately equal to that of penis, external surface of distal half glandular. Base of penis bulges into atrium. Vagina short, approximately 15% of penial length. Spermathecal duct diameter greater than that of free oviduct, slight taper toward spermatheca. Spermatheca round. Dart sac (with dart) smaller than spermatheca. Penis straight, basal diameter one third of length, slight taper to junction with vas deferens; penial sheath reaches to junction of penis with vas deferens. Internally,



Figures 7, 8. Internal penial anatomy. **7.** *Philomycus virginicus*. **8.** *Philomycus sellatus*. Scale bar = 10 mm. Cut surfaces indicated by oblique lines in all drawings. A: atrium, DS: dart sac, P: penis, PR: penial retractor, PS: penial sheath, VD: vas deferens.



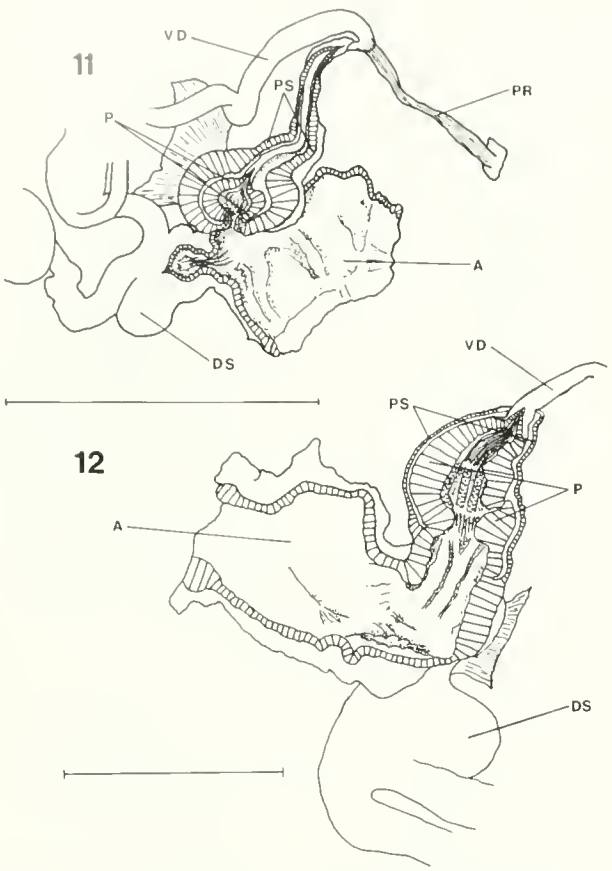
Figures 9, 10. Genitalia. **9.** *Philomycus bisdosus*. Scale bar = 10 mm. **10.** *Philomycus carolinianus*. Scale bar = 5 mm. A: atrium, AG: albumen gland, AR: accessory retractor, DS: dart sac, FO: free oviduct, G: gonad, GP: genital pore, HD: hermaphroditic duct, P: penis, PR: penial retractor, S: spermatheca, V: vagina, VD: vas deferens.

penis with 4–6 pustulose ridges, a basal pustulose circular ridge sets off distal parts of the penis from its opening into the atrium. Vas deferens encircles distal end of penis, entering penis terminally. Vas deferens length approximately 3.3 times that of penis, approximately same diameter throughout its length. Penial retractor muscle maximum width one third that of diameter of distal end of penis but broader at its distal end, length approximately one third that of penis. Accessory retractor muscle absent or not distinguishable from typical connective tissues.

Table 1. Measurements (mm) of selected reproductive organs of species of *Philomycus*. Means with std. deviation and ranges are shown.

	P. sellatus (4)*	*P. virginicus* (4)*	*P. carolinianus* (5)*	*P. bisdosus* (2)*	*P. flexuolaris* (2)*	*P. togatus* (2)*
Length of penis	13.1 (1.82) 11.0–14.2	5.8 (0.66) 5.4–6.8	6.0 (0.61) 5.4–7.0	7.1 (0.00) 7.1	7.3 (0.35) 7.0–7.5	12.9 (2.33) 11.2–14.5
Diameter of penis (atrial end)	4.4 (0.49) 4.1–5.0	3.7 (1.07) 2.7–5.0	2.2 (0.29) 1.9–2.7	3.0 (0.07) 2.9–3.0	2.8 (0.64) 2.3–3.2	3.3 (0.42) 3.0–3.6
Length of vagina	1.2 (0.15) 1.0–1.3	0.8 (0.29) 0.5–1.0	1.5 (0.41) 1.1–2.2	1.1 (0.49) 0.7–1.4	1.6 (0.35) 1.3–1.8	3.1 (1.70) 1.9–4.3
Length of free oviduct	8.8 (1.50) 7.8–10.5	10.2 (1.87) 8.9–12.9	7.7 (1.44) 6.2–10.0	7.6 (0.62) 6.9–8.1	7.6 (0.64) 7.1–8.0	7.2 (0.28) 7.0–7.4
Length of vas deferens	57.5 (4.77) 52.0–60.5	21.1 (2.11) 18.8–23.0	38.1 (4.96) 33.8–45.1	19.1 (1.02) 17.9–19.8	24.2 (3.04) 22.0–26.3	34.0 (0.71) 33.5–34.5

* Number of specimens measured



Figures 11, 12. Internal penial anatomy. **11.** *Philomycus bisdosus*. Scale bar = 10 mm. **12.** *Philomycus carolinianus*. Scale bar = 5 mm. A: atrium, DS: dart sac, P: penis, PR: penial retractor, PS: penial sheath, VD: vas deferens.

DISCUSSION

When Hubricht (1972) described *Philomycus sellatus*, he noted that, based upon the posterior half of the mantle, it ". . .is most closely related to *P. carolinianus* (Bosc).", with which "It sometimes occurs. . .". However, the black transverse band near the anterior end of the mantle of *P. sellatus* (figures 3, 4), which is not present on *P. carolinianus* (Pilsbry, 1948 p.748), easily separates the two species in the field. Their reproductive systems (figures 6, 10) are also distinct. The shape of the penes and their internal anatomies (figures 8, 12) are clearly different. *Philomycus carolinianus* lacks the two internal constrictions in the penial wall that are found in *P. sellatus*, and the internal penial pilasters are smaller and more numerous in *P. carolinianus* than in *P. sellatus*. Additionally, the penis and vas deferens of *P. sellatus* are nearly twice as long as those of *P. carolinianus* (Table 1). Indeed, the black anterior transverse band on the mantle and the two constrictions in the penial wall are characteristics unique to *P. sellatus*.

Hubricht (1953) noted that *Philomycus virginicus* was found associated with *P. flexuolaris* (Rafinesque, 1820) and *P. togatus* (Gould, 1841) (as *P. carolinianus collinus* in Hubricht's 1953 article). Among these taxa, only *P. virginicus* has the transverse chevron pattern on the mantle (figures 1, 2) and is thus easily separated from the others in the field. In addition, measurements of the reproductive systems of *P. flexuolaris* and *P. togatus* demonstrated several differences from that of *P. virginicus* (Table 1). The penis and vagina of *P. virginicus* are shorter than those of *P. flexuolaris*; the free oviduct of *P. virginicus* is much longer than that of *P. flexuolaris*. *Philomycus togatus* has a much longer penis, vagina, and vas deferens than *P. virginicus*; the free oviduct of *P. virginicus* is longer than that of *P. togatus* (Table 1). Branson (1968), in reference to *P. virginicus* and *P. bisdosus* (figures 5, 9), stated that "The genitalia of the two species also differ.", but no figures nor measurements were included. Branson (1969) listed some differences between the reproductive anatomies of these latter two species, but again without figures or measurements. Figures 7 and 11 show clearly the differences in the shape of the penis and the internal penial anatomy of these two species, and the free oviduct of *P. virginicus* is nearly 1.5 times the length of the *P. bisdosus* oviduct (Table 1). In addition, *P. bisdosus* lacks the anterior to posterior transverse chevrons on the mantle. Comparisons with previous studies of reproductive anatomy in species of *Philomycus* (Fairbanks, 1986, 1989; Pilsbry, 1948) confirmed that the internal surface of the penis of *P. virginicus* is unique in having a basal circular pustulose ridge at the atrial end.

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Two Confusing Indo-Pacific Cerithiids

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ABSTRACT

Cerithium zebrum Kiener, 1841 and *Cerithium boeticum* Pease, 1860, although originally described as *Cerithium* species, had been allocated to *Bittium* Gray, 1847, in the recent literature. Anatomical investigation has shown that these two species do not have the characters of *Bittium* species, but are are more like *Cerithium* taxa, except for their small size. *Cerithium zebrum* is distinguished from *Cerithium boeticum*, based on morphological characters derived from the shell, radula and soft anatomy. Synonymies, descriptions and a discussion of the differences between the species are presented.

Key Words: Cerithium, *Bittium*, morphology, anatomy, taxonomy.

INTRODUCTION

Small-shelled cerithiids are difficult to identify to the species-level, particularly poorly-known taxa from the Indo-Pacific region. Generic and sometimes familial determinations of these small snails are likewise difficult and controversal, and in most museum collections many small-sized cerithiids are grouped together and loosely attributed to the genus *Bittium* Gray, 1847.

During a recent generic review of the *Bittium*-group the anatomy of a number of "*Bittium*" species were examined. One of the taxa studied is "*Bittium*" *zebrum* (Kiener, 1841), a common species throughout the Indo-Pacific region that is extremely variably in sculpture and color pattern. As expected in a common, widely-distributed species comprising many sculptural phenotypes and color morphs, "*Bittium*" *zebrum* has been zealously overnamed by authors, as a perusal of its synonymy will testify.

When living "*Bittium*" *zebrum* specimens from Guam, Enewetak, and Hawaii were examined it was discovered that none of these snails had an epipodial skirt, characteristic of members of Bittiinae. Moreover, there was no spermatophore bursa present in the lateral lamina of the pallial oviduct, a feature distinctive of the *Bittium*-group. These animals are thus transferred from *Bittium* to *Cerithium* Bruguière.

Further comparison of the Hawaiian specimens of "*Bittium*" *zebrum* with those from other Indo-Pacific regions revealed that there are considerable morphological differences between the populations: the shells, radula and anatomy of the Hawaiian specimens are quite distinct from those of *zebrum* specimens from elsewhere. Subsequent careful examination of many museum lots of *Cerithium zebrum* revealed that most lots of Hawaiian specimens comprised mixtures of two species: the first having a typical *zebrum* phenotype, and the second, more common, species having a different shell physiognomy. It became apparent that the second species is *Cerithium boeticum* Pease, 1860, named from the Hawaiian Islands and subsequently considered to be conspecific with "*Bittium*" *zebrum* by Kay (1979).

This paper addresses the differences between the two species, describes and presents a synonymy of each, and delineates the characters separating and distinguishing them. *Cerithium boeticum* is recognized as a valid species, different from *Cerithium zebrum*, and is shown to be endemic to the Hawaiian Islands.

MATERIALS AND METHODS

Living specimens of *Cerithium zebrum* were studied at Enewetak Atoll, Marshall Islands, and at the University of Guam Marine Laboratory at Pago Bay, Guam. *Cerithium boeticum* was collected from shallow, subtidal coral rubble in Kewalo Basin, Honolulu, placed in aquaria and observed at the Kewalo Laboratory of the Hawaiian Biomedical Research Laboratory, University of Hawaii, Honolulu, Hawaii. Both species were observed and dissected under water in wax-filled petri dishes using a Wild M-5 dissecting microscope. Methylene blue was used to enhance anatomical features during dissection. Protoconchs, shells, opercula and radulae were studied with an Hitachi S-570 scanning electron microscope. The types of both species and their synonymous nomina were examined and are discussed below. Many museum lots were examined in order to establish the range of phenotypic variation in the shells of each species. Measurements and meristic data of shells were taken using randomly selected specimens from locations throughout the geographic range of each species.

Material examined: *Cerithium boeticum*. **HAWAIIAN ISLANDS:** (USNM 343522); Oahu (USNM 12916, types); Honolulu, Oahu (USNM 335496, 335499, 335497, 335498, 767506); Waikiki Marine Lab, Honolulu, Oahu (USNM 633002); Kewalo Basin, Honolulu, Oahu (USNM 857099); Honolulu Reef, Oahu (USNM 335289); Quarantine Island, Honolulu, Oahu (USNM 339349, 339342); Waikiki, Oahu (USNM 343514, 343515, 343519); off Waikiki, Honolulu, Oahu (USNM 339118); Kewalo Basin, Honolulu, Oahu, Hawaii (USNM 857099); Diamond Head, Honolulu, Oahu (USNM 339339, 343510); Mokapu Beach, Oahu (USMN 484570); Maunalua Beach, Oahu (USNM 428173, 428174, 428207, 343520, 343511); Mokoloe Island, Oahu (USNM 339343, 343512); Kaneohe Bay, Oahu (USNM 472057, 472058, 343513); Coconut Island, Kaneohe Bay, Oahu (USNM 771362, 771556); Hospital Point, Pearl Harbor, Oahu (USNM 497938); Pearl Harbor, Oahu (USNM 484455, 428234, 341308); Pupukea Beach, Oahu (USNM 484689); Kahana Bay, Oahu (USNM 777967); Kahala, Oahu (USNM 33951, 339928); Kahala Beach, Koko Head, Oahu (USNM 343546); Keoke River, Hawaii (USNM 252339, 252338, 252336); Keokea, Hawaii (USNM 337592); Keokea, Hilo, Hawaii (USNM 339340, 339340); Hilo, Hawaii (USNM 612281); Kuhio B., Hilo, Hawaii (USNM 339125); Honaunau, Hawaii (USNM 343517); 5 mi SW Kapoho, Hawaii (USNM 409081, 409095); Lanai (USNM 612425); Mauele, Lanai (USNM 339341); Hanalei, Kauai (USNM 340692); Midway Island (USNM 790897, 790898); Frigate Point, Sand Island (USNM 678064).

Cerithium zebrum. **MAURITIUS:** (USNM 91247, 91069, 91070); Flicq-en-Flacq, Arsenal Bay (USNM 716523). **SEYCHELLES:** Aldabra Atoll, Île Picard (USNM 837490). **COCOS (KEELING) ISLANDS:** Alor Pinyu, NW side of West Island (USNM 656435). **AUSTRALIA:** Heron Island, Queensland (USNM 8540174); Watson's Bay, Lizard Island, Queensland (USNM 783381). **RYUKYU ISLANDS:** Osima, Osumi (USNM 343873); Odomaria, Okinawa, Shima (USNM 488199); Yenoshima (USNM 228222); Chichyima, Ogasawara (USNM 175587). **BONIN ISLANDS:** (USNM 36950, 343874). **PHILIPPINES:** Jamelo Bay, Luzon (USNM 935351). **MARIANAS:** Saipan (USNM 486824, 486823, 486795); Guam (USNM 851104, 851104); Pago Bay, Guam (USNM 774778); Apra Bay, Guam (USNM 240110); Orote Point, Orote Cliffs, Guam (USNM 854036). **CAROLINES:** Moen Island, Truk Lagoon (USNM 842615); Reef at Mutunlik, Kusaie Island (USNM 609487). **LOYALTY ISLANDS:** (USNM 253564); Lifu (USNM 423278, 423260, 423210, 423282, 423281, 423261, 423325, 423283). **FIJI:** Rat Tail Passage, Suva Reef (USNM 824808); SAMOA: Pago Pago (USNM 361535, 361536); Ofu, Manu'a Group (USNM 380968, 380965, 380967, 380969, 380962, 380963, 380960, 380966). **MARSHALL ISLANDS:** Enewetak (USNM 432415, 770725, 542726); Rennit Island, Enewetak (USNM 542809); Fred, Enewetak (USNM 770687); Aaraanbiru Island, Enewetak (USNM 582227, 582265); Teiteiripucoki Island, Enewetak (USNM 581543); Girunien Island, Enewetak (USNM 581534); Engebi Island, Enewetak (USNM 743869); Rijoru Island, Enewetak (USNM 581555); E. Rigili Island, Enewetak (USNM 581923); between Rigili and E. Rigili Islands (USNM 581576, 581575); Ailuk Island, Ailuk Atoll (USNM 615133); Lae Island, Lae Atoll (USNM 614896); Bock Island, Rongerik (USNM 594660); Enyvertok, Rongerik (USNM 583519); 4 mi. W Bikini Islands (USNM 586086); Bikini (USNM 583949, 585185); Bokororyuru, Bikini (USNM 583883, 583884); Namu Island, Bikini (USNM 580542); Enyu Island, Bikini (USNM 580945); Eninman Island, Bikini (USNM 586897); Pigeniyarayro, Rongelap (USNM 585588, 585327); Kabelle Island, Rongelap (USNM 582405, 582388, 582125, Burok, Rongelap (USNM 583989); NIUE: Opaahi, S. of Alofi (USNM 854054); Alofi (USNM 854046); Tuapa (USNM 858164); Tuapa, Avaiki Cave (USNM 854055). **COOK ISLANDS:** Mauke Island (USNM 598174). **SOCIETY ISLANDS:** Reao Id (USNM 5573, holotype); Makatea, Tuamotu Archipelago, N Timae Harbor (USNM 819895); Arue, Papeete, Tahiti (USNM 775927); Mahina, Tahiti (USNM 797267, 791372); Tahiti (USNM 91068). **WALLIS & FUTUNA ISLANDS:** outer reef E of Nukuhifala (USNM 676427); Henderson Id (G. Pauley coll.). **NIUE:** off warf, Alofi (USNM 854046); Avaiki Cave, Tnapa (USNM 854055); Tuapa (USNM 858167); Opaahi, S Alofi (USNM 854054). **HAWAII:** French Frigate Shoals (ANSP 195368, 195384); Midway (USNM 790897); Honaunau, Hawaii (USNM 343509); Keokea, Hilo, Hawaii (USNM 339353).

Abbreviations: BMNH = British Museum (Natural History); MNHNP = Museum National d'Histoire Naturelle, Paris; NMW = National Museum, Wales; SEM = scanning electron microscope; USNM = United States National Museum, Smithsonian Institution, Washington, D.C.

RESULTS

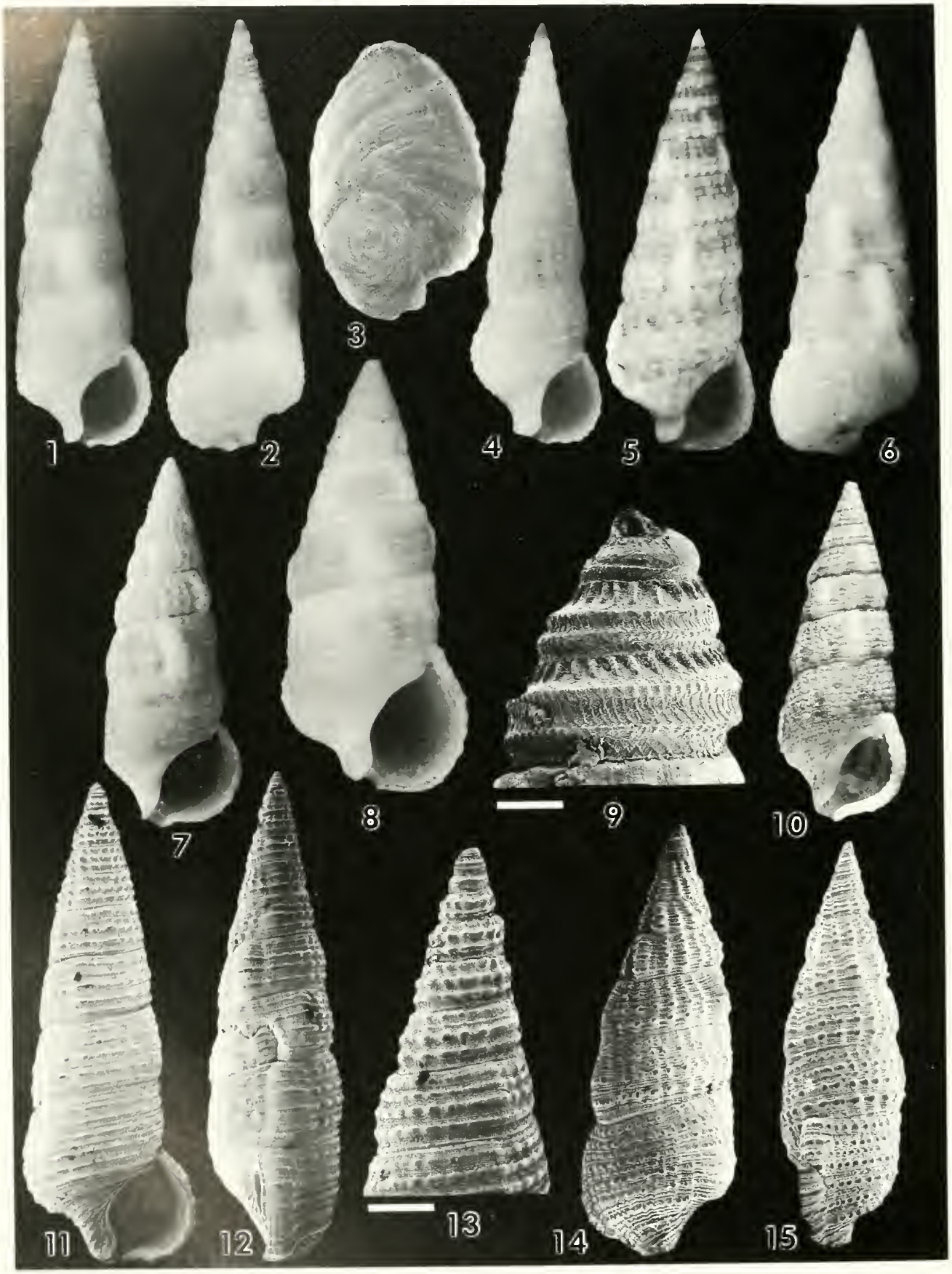
Descriptions (Tables 1 & 2, Figs. 1–28), synonymies, and discussions of both species are presented below, followed by a table identifying the characters separating the two species (Table 3).

Cerithium zebrum Kiener, 1841

Cerithium zebrum Kiener, 1841:71, pl. 25, fig. 4 (holotype, MNHNP; type locality, Indian Ocean, Mauritius). Sowerby,1855:875–876, pl. 183, figs. 207–209; 1865, pl. 19, fig.136; Tryon, 1887: 138, pl. 26, figs. 78–82; Kobelt, 1898:210–211, pl. 39, figs. 7–10; Hedley, 1899:434; Vignal, 1903:21–22, pl. 2, fig. 1; Schepman, 1909:162; Dautzenberg & Bouge, 1933:313.

Cerithium janthinum Gould, 1849:121 (holotype, USNM 5573, 8.5 × 3.9 mm; type loclaity, Clermont Tonnere [Reao Id, Tuamotus]; 1852:152, pl. 10, fig. 173a-b; 1862:63; Johnson, 1964:95.

Cerithium zebrum var. *dilectum* C.B. Adams in Sowerby, 1855: 896, pl. 33, fig. 207• (15 syntypes, BMNH 1969349; type locality, Galapagos [in error]); Vignal, 1903:22–23, pl. 2, fig. 5.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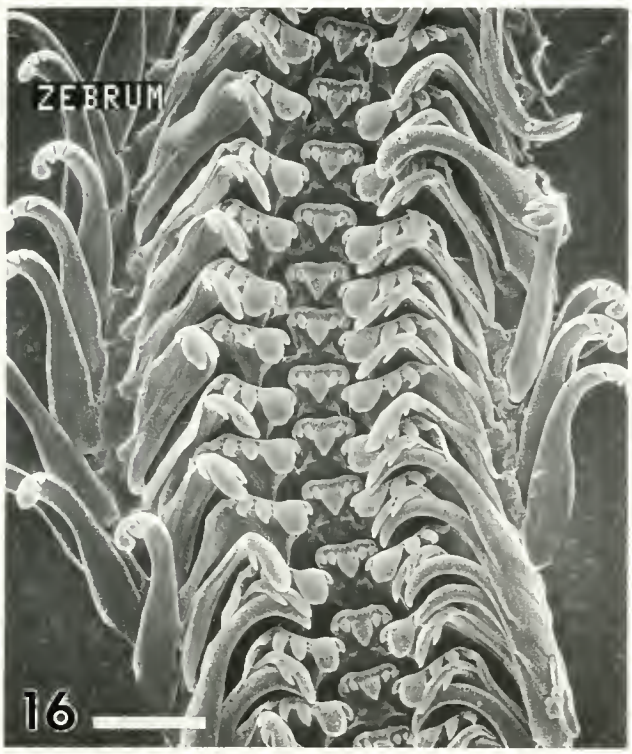

Figs. 16–17. Scanning electron micrographs of radula of *Cerithium zebrum* Kiener, Pago Bay, Guam (USNM 774778); **16.** view of mid-section of radula, bar = 36 μm; **17.** half row showing details of rachidian, lateral and marginal teeth, bar = 29 μm.

Cerithium delectum (sic) A. Adams. Sowerby, 1865, pl. 16, fig 112 a-c; Vignal, 1903:23.

Cerithium unilineatum Pease, 1860:432 (lectotype, BMNH 19622798, 5.5 × 3 mm, 2 paralectotypes BMNH 1962799; type locality, Sandwich Ids [Hawaiian Ids]). Sowerby, 1866, pl. 15, fig.99; Tryon, 1887:138, pl. 26, fig. 86; Kobelt, 1898: 224, pl.29, fig. 18.

Cerithium stigmosum Gould, 1861:386 (holotype, ?; type locality, Bonin Ids) 1862:141; Johnson, 1964:152.

Cerithium aspersum Deshayes, 1863:97–98, pl. 11, figs. 16–18 (lectotype, here selected, MNHNP, 8.8 mm, 4 paralectotypes, MNHNP; type locality, Réunion).

Cerithium Crossii Deshayes, 1863:96, pl. 11, figs. 12–14 (lectotype, here selected, MNHNP, 8.4 mm, 3 paralectotypes, MNHNP; type locality, Réunion; *not Cerithium crosseanum* Tiberi, 1863 [= *Cerithioipsis subcylindricum* (Brusina)], *nor Cerithium maillardi* Crosse, 1863 [unnecessary replacement name for *Cerithium crosseanum* Tiberi].

Cerithium dichroum Melvill & Standen, 1895:115, fig. (6 syntypes NMW 55158200; type locality, Lifu, Loyalty Ids)

Cerithium zebrum var. *pulchra* Vignal, 1903:22, pl. 2, fig. 2 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *trifasciata* Vignal, 1903:22, pl. 2, fig 3 (type, MNHNP; type locality, Isle of Pines, New Caledonia).

Cerithium zebrum var. *attenuata* Vignal, 1903:22, pl. 2, fig. 4 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:313.

Cerithium zebrum var. *undulata* Dautzenberg & Bouge, 1933: 316 (Type, MNHNP; type locality, Tuamotus).

Cerithium zebrum var. *rosea* Vignal, 1903:24, pl. 2, fig. 6 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *cinerea* Vignal, 1903:24, pl. 2, fig. 7 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:314.

Cerithium zebrum var. *nivea* Vignal, 1903:24, pl. 2, fig. 8 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *bilineata* Vignal, 1903:25, pl. 2, fig. 10

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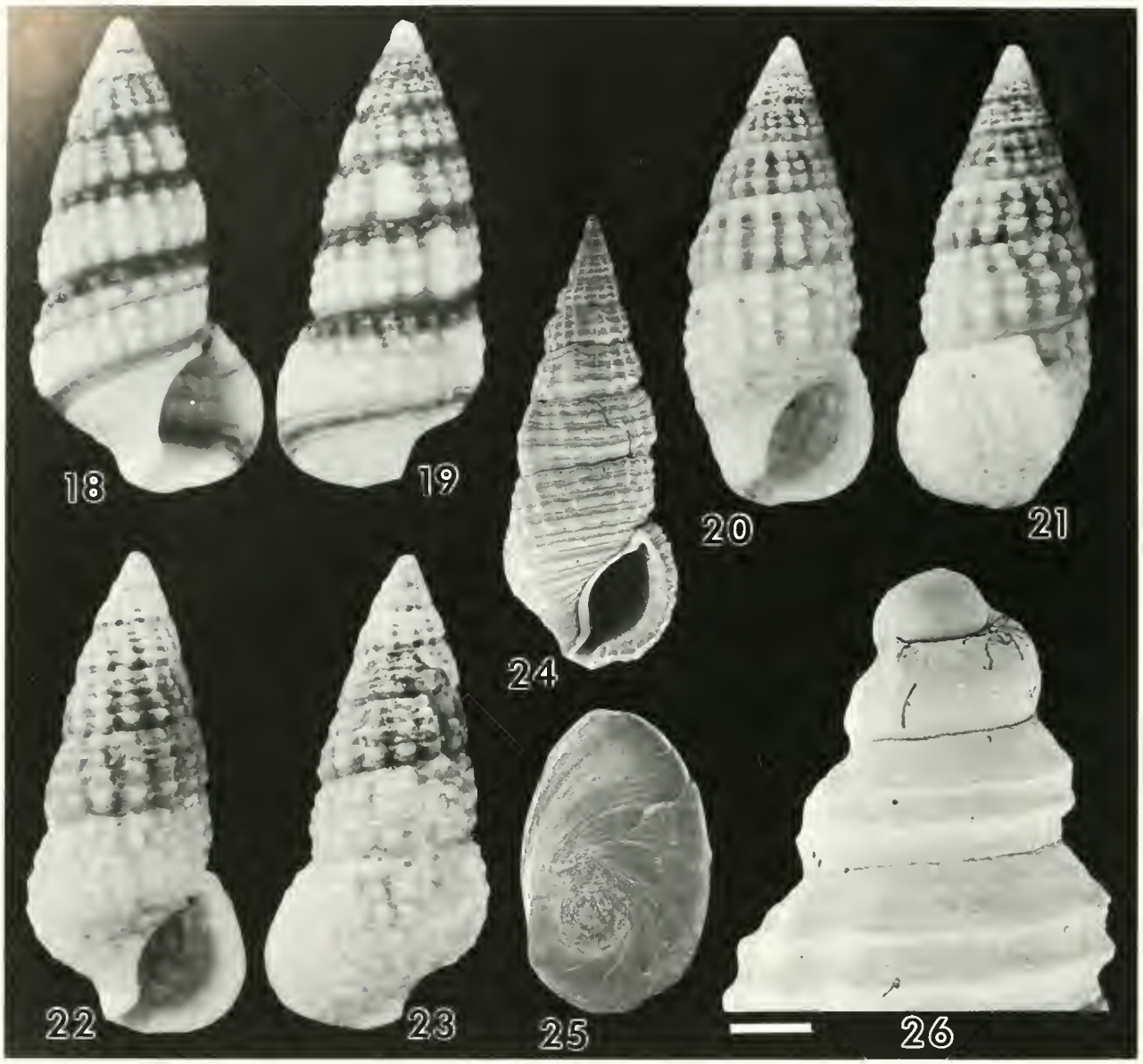
Figs. 1–15. Cerithium zebrum Kiener, showing shell variation and types of synonymous nominal taxa. **1–2.** Orote Point, Guam, 7.9 mm length; **3.** operculum, 1.3 mm length (USNM 854036); **4.** Orote Point, Guam, 7.5 mm length (USNM 854036); **5.** Pago Bay, Guam, 7.8 mm length (USNM 774778); **6.** Enewetak Atoll, Marshall Islands, 7.9 mm length (USNM 770725); **7.** lectotype of *Cerithium crossii* Deshayes, Réunion (MNHNP), ; **8.** Holotype of *Cerithium janthinum* Gould, Reao, Tuamotns (USNM 5573); **9.** SEM of protoconch, bar = 70 μm; **10.** lectotype of *Cerithium aspersum* Deshayes, Réunion, 8.2 mm (MNHNP); **11–12.** Pago Bay, Guam, apertural and right lateral views under SEM, showing sculptural details, 5.8 mm length (USNM 774778); **13.** sculptnre of early whorls, SEM, bar = 0.9 mm; **14–15.** Pago Bay, Guam, dorsal and right lateral views under SEM, 5.8 mm length (USNM 774778).



Figs. 18–26. Cerithium boeticum Pease, from Kewalo Basin, Honolulu, Oahu, Hawaii, showing shell variability (USNM 857099). **18–19.** Strongly banded morph, 5.8 mm length; **20–21.** white morph, 5.7 mm length; **22–23.** 5.7 mm length; **24.** scanning electron micrograph showing sculptural details and aperture, 4.9 mm length; **25.** operculum, 2 mm length; **26.** SEM of protoconch and early whorl sculpture, bar = 88 μm

(type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:314.

Cerithium zebrum var. *trilineata* Vignal, 1903:25, pl. 2, fig. 11 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *ornata* Vignal, 1903:26, pl. 2, fig. 13 (type, MNHNP; type locality, Isle of Pines, New Caledonia).

Cerithium zebrum var. *sticta* Vignal, 1903:26, pl. 2, fig. 14 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *mutimaculata* Vignal, 1903:26, pl. 2, fig. 15 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:315.

Cerithium zebrum var. *maculata* Vignal, 1903:26, pl. 2, lig. 16 (type, MNHNP; type locality, Isle of Pines, New Caledonia); Dautzenberg & Bouge, 1933:314.

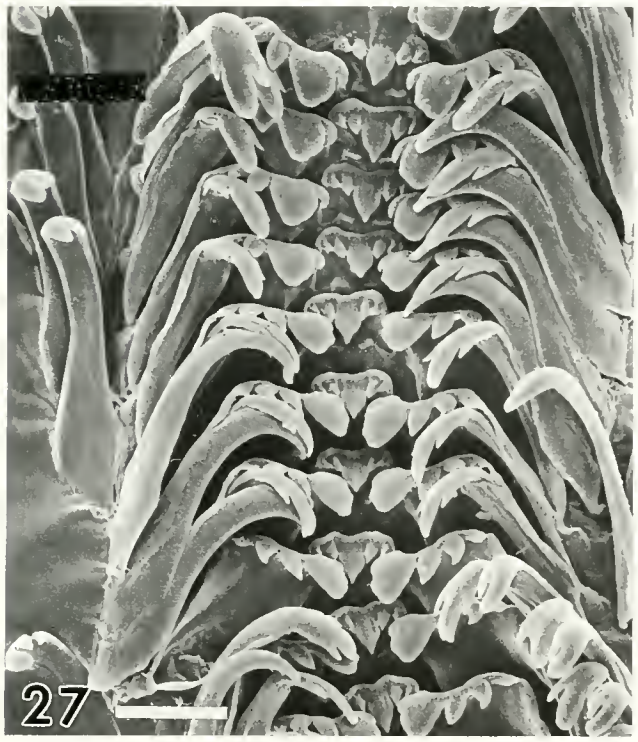
Cerithium zebrum var. *unimaculata* Vignal, 1903:27, pl. 2 fig. 17 (type, MNHNP; type locality, Isle of Pines, New Caledonia).

Cerithium zebrum var. *aspersa* Deshayes. Dautzenberg & Bouge, 1933:314.

Bittium zebrum (Kiener) Cernohorsky, 1972:69–70, pl. 14, fig. 10; Salvat & Rives, 1975:272, fig. 74.

Bittium zebrum (Kiener) Kay, 1979:120, figs. 45b-c (not *Bittium zebrum* (Kiener), is *Cerithium boeticum* Pease 1860).

Description: Shell (Figs. 1–15; Table 1): turreted, elongate, attaining 10.4 mm length, 3.2 mm width, and comprising about 9 weakly inflated to flat-sided whorls. Pro-



Figs. 27–28. Scanning electron micrographs of radula of *Cerithium boeticum* Pease, Kewalo Basin, Honolulu, Oahu, Hawaii (USNM 857099). **27.** general view of mid-radular ribbon, bar = 25 μm; **28.** detail of rachidian tooth, bar = 9 μm.

toconch (Fig. 9) comprising 3 whorls; protoconch 1 nearly smooth, sculptured with suprasutural spiral cord; protoconch 2 sculptured with series of subsutural plaits followed by two strong spiral cords, criss-crossed by minute lirae up to anterior suture. Early whorls (Fig. 13) sculptured with 3 beaded spiral cords. Adult whorls sculptured with 4 beaded, major spiral cords each separated from one another by one fine spiral lira. Penultimate whorl with 5 beaded spiral cords, having about 26 spiral beads; beads frequently aligned to form weak axial riblets. Body whorl with 11–12 beaded spiral cords and fine spiral lirae. Suture weakly defined. Strong white varices randomly placed on whorls; largest varix on right dorsal side of body whorl. Aperture circular-ovate, a little over one-fourth the shell length. Outer lip thick, relatively smooth, weakly crenulate at inner edge; columella concave with weak callus. Anterior canal short, but pronounced, oriented at 45 degree angle to shell axis. Weak siphonal constriction. Anal canal small, defined by small parietal plait. Shell color white with pink early whorls and adult whorls with brown, tan, rose blotches and spiral stripes, bands, or dots. Aperture white. Periostracum thin, light tan.

Animal: Headfoot white, flecked with opaque white, rose or tan. Snout, mantle edge and siphon yellow. Mantle edge with short yellow papillae. Snout long, extensible, having bilobed tip (lips). Operculum (Fig. 3) tan, corneous, ovate, paucispiral with eccentric nucleus. Lateral epipodial skirt and operculiferous lobe absent. Osphradium bipectinate, with weakly-defined pectins. Radula (Figs. 16–17) short, about one-ninth the shell length. Rachidian tooth (Fig. 17) height equals length, having hourglass-shaped basal plate with spade-shaped basal projection and two small basal lateral butresses; cutting edge with large, pointed central cusp flanked by two small pointed denticles on each side. Lateral tooth with rectangular basal plate having long lateral projection and

Table 1. Shell statistics for *Cerithium zebrum* (measurements in mm).

Statistic (n = 17)	$\bar{x}$	sd	Range
Length	7.3	1.5	4.2–10.35
Width	2.4	0.4	1.8–3.2
Aperture length	1.3	0.3	0.8–1.8
Number of whorls	9.2	1.6	7–13
Number spiral beads	26.3	6	19–44

Table 2. Shell statistics for *Cerithium boeticum* (measurements in mm).

Statistic (n = 17)	$\bar{x}$	sd	Range
Length	6.1	1.8	2.4–10.5
Width	2.3	0.8	1.2–4.6
Aperture length	1.7	0.7	0.8–2.4
Number of whorls	8.0	0.9	6–9
Number axial beads	17.4	1.7	14–20

thick central buttress; cutting edge with one weak inner denticle, large spoon-shaped cusp, and three outer denticles. Marginal teeth spatulate, curved at tips; inner marginal tooth with three pointed inner denticles, large central cusp and two outer denticles; outer marginal tooth same but without outer denticles. Esophageal gland present; stomach large; style sac and crystalline style long, about one-third stomach length.

Synonymic remarks: This species has been the recipient of 23 names, all of which have been based on conchological characters and/or differences in shell pigmentation. It is obvious that the authors of these nomina did not employ a modern species concept and failed to recognize the full range of intraspecific variation when proposing these taxa. Examination of the types of the synonymous nomina revealed no significant differences in shell sculpture from that of *Cerithium zebrum* (Kiener); indeed, the nomina proposed by Vignal (1903) as varieties of *Cerithium zebrum* Kiener were based on mere intraspecific color variation, as Vignal (1903) clearly stated. The holotype of *Cerithium janthinum* Gould (see Fig. 8) is merely a worn, very wide morph of *Cerithium zebrum*. Sowerby (1855) introduced the name *dilectum* in the *Thesaurus* as a variety of *Cerithium zebrum* Kiener, but the new taxon was indicated only by the italicized name in his "Alphabetical list of species", on p. 896. The name *dilectum* was initially listed on p. 117 as a synonym of *Cerithium zebrum*, and the legend for the figures of *Cerithium zebrum* (figs. 107–109) does not include the name *dilectum*, although one of the figures has an asterix (fig. 207•), which presumably is meant to indicate the varietal taxon, *dilectum*. *Cerithium aspersum* Deshayes is a highly sculptured morph of *C. zebrum*, as illustrated by the lectotype (Fig. 10). *Cerithium erossi* Deshayes, 1863, which as shown by the lectotype (Fig. 7), is conspecific with *Cerithium zebrum*, was incorrectly considered by Crosse (1863) as a homonym of *Cerithium crosseanum* Tiberi, 1863, a *Cerithiopsis* species, and was given an unnecessary replacement name, *Cerithium maillardi* Crosse, 1863. *Cerithium boeticum* Pease erroneously has been considered conspecific with *Cerithium zebrum* Kiener by Kay (1979). For a discussion of this issue, see the discussion under *Cerithium boeticum*.

Discussion: *Cerithium zebrum* is a very common species, frequently found in the upper intertidal zone among rubble and algae on benches and platforms associated with fringing coral reefs of atolls and islands throughout the Indo-Pacific. In the Hawaiian Islands is also occurs in deeper waters (Kay, pers. com.). It is characterized by an elongate, tapering shell, sculptured with many fine beaded spiral cords and with numerous broad, white, randomly-placed varices. *Cerithium zebrum* is a colorful species, having a rose-colored apex capped with a dark brown protoconch (see Figs. 1–2,4,6). The adult whorls are frequently white or light pink with tan blotches or with brown and tan bands. While the species varies greatly in color pattern, shell sculpture is relatively stable throughout its range. Banded varieties of *Cerithium zebrum* may be confused with banded morphs of *Cerithium boeticum*, but the latter species has a more coarsely sculptured shell with stronger axial ribs, a more deeply incised suture, and a thick outer apertural lip (see Figs. 18–26). The animal (headfoot), in contrast to the brightly pigmented shell, is a uniform white overlain by opaque white spots, although some shells may also be white.

In contrast to the lecithotrophic development seen in *Cerithium boeticum*, *Cerithium zebrum* undergoes a lengthy planktotrophic larval phase and has an elaborately sculptured protoconch (Fig. 9) with a deep sinusigeral notch indicative of this developmental mode. The operculum of *Cerithium zebrum* is slightly more ovate, thicker and opaque, and has fewer spirals than that of *Cerithium boeticum*.

Cerithium zebrum occurs from Henderson Id., in the Pitcairn Group, throughout French Polynesia and the Hawaiian Islands, and westward throughout the tropical Pacific from Queensland, Australia, north to the Ryukyus. It is found throughout the archipelagos of southeast Asia and in suitable localities in the Indian Ocean. Indeed, specimens from Tamarin Bay, Mauritius (ANSP 273492) look very much like those found in Tahiti (Fig. 6) and Guam (Figs. 1–2, 4–5). While *Cerithium zebrum* has occasionally been collected in assemblages from depths greater than 10 m around the main, volcanic Hawaiian Islands (Kay, in lit.), it is more common on the shallow reefs of the Northwestern Hawaiian Islands at French Frigate Shoals (ANSP 195368, 195384) and Midway (USNM 790897).

To my knowledge, *Cerithium zebrum* has not been recorded as a fossil.

Cerithium boeticum Pease, 1860

Cerithium pusillum Gould, 1851: 120–121 (holotype, USNM 5572, 4 paratypes, MCZ 216606; type locality, Sandwich Ids [Hawaiian Ids]; *not Cerithium pusillum* Pfeiffer, 1840, *nor* Dunker,1859); Gould, 1852:150, pl. 10, fig. 172a-b; Gould, 1862:62; Dunker, 1882:108.

Cerithium boeticum Pease, 1860: 433 (lectotype [Kay, 1965], BMNH 1962802, 6 × 2.5 mm, 5 paralectotypes, BMNH 1962803; type locality, Sandwich Ids [Hawaiian Ids]); Sowerby, 1866 "*baeticum*", pl. 12, fig. 327; 1866b, pl. 16, fig. 114; Tryon, 1887:143, pl. 27, fig. 26; Kobelt, 1898:236, pl. 41, fig. 14; Kay, 1965:48–49, pl. 10, fig. 8.

Bittium pusillum (Gould) Johnson, 1964: 136; Kay, 1979:120 (*not Bittium pusillum* [Dunker, 1859]).

Bittium zebrum (Kiener) Kay, 1979: 120, fig. 45b-c (*not zebrum* Kiener, 1841, *is Bittium pusillum* [Gould, 1849]).

Bittium boeticum unilineatum Pse. (sic). Mant, 1923: 121.

Bittium boeticum Pils. & Va. (sic). Mant, 1923: 121.

Description: Shell (Figs. 18–24, 26; Table 2): Shell solid, turreted, reaching 10.5 mm length and 4.6 mm width, comprising about 8 convex whorls. Protoconch (Fig. 26) one whorl, smooth with straight lip. Early whorls sculptured with two spiral cords and weak axial ribs. Penultimate whorl sculptured with 4 major beaded, spiral cords

each separated from the other with weak spiral lirae, and each bearing about 17 beads alined to form 17 strong axial ribs. Body whorl large, sculptured with 9 spiral beaded cords and weak spiral lirae. Several varices randomly distributed on shell, strongest opposite outer lip of aperture. Suture deeply impressed. Aperture oval-elongate, a little over one-third the shell length. Anterior canal short, well-defined, oriented at 45 degree angle to shell axis; outer lip thick, strongly denticulate along inner edge; columella concave with moderate callus. Anal canal weak, defined by parietal plait.

Animal: Headfoot without lateral epipodial skirt; weakly scalloped operculiferous lobe present. Operculum (Fig. 25) corneous, very thin, transparent and paucispiral with slightly eccentric nucleus. Osphradium very large, about one-half width of ctenidium, strongly bipectinate with large pectins. Hypobranchial gland well-developed. Medial lamina of pallial oviduct with spermatophore bursa and large seminal receptacle. Radula (Figs. 27–28) very short, about one-twelfth the shell length. Rachidian tooth (Fig. 28) wider than tall, hourglass-shaped, with basal plate having short basal projection and two small lateral buttresses; cutting edge with spade-shaped central cusp flanked on each side with three, sometimes two, small pointed denticles. Lateral tooth with rectangular basal plate having long lateral projection and short basal buttress; cutting edge with small inner denticle, long spoon-shaped major cusp, and two, sometimes three, outer pointed denticles. Marginal teeth elongate, spatulate with curved tips; inner marginal tooth with two inner denticles long, major central cusp and one outer denticle; outer marginal tooth same but without outer denticle.

Synonymic remarks: *Cerithium boeticum* has been confused with several other taxa assigned to *Cerithium* or *Bittium* by authors. The earliest name for the species is *Cerithium pusillum* Gould, 1851, but as this name is preoccupied, the next available valid name is *Cerithium boeticum* Pease, 1860. Although the figures subsequently presented by Gould (1852, pl. 10, figs. 172a-b) for *Cerithium pusillum* are not very good, the holotype (USNM 5572) clearly shows that this taxon is different from *Cerithium zebrum* Kiener, with which it has been confused (e.g., Kay, 1979: 120). *Cerithium pusillum* Dunker, 1859, and *Cerithium pusillum* Gould, 1851, are different species, but as both taxa have been referred to *Bittium* by authors, some confusion has developed about their identity.

Cerithium boeticum Pease is a name seldom mentioned in the literature and has not been a well-understood species. Kay (1965) designated a lectotype and five paralectotypes from the original type lot of six beach-worn specimens, but her illustration of the lectotype (1965, pl. 10, fig. 8) is poor and is not helpful in clarifying the concept of the species. Kay (1979) subsequently placed this taxon into the synonymy of *Cerithium zebrum*, a species with a wide Indo-Pacific distribution. Further confusion has developed because another Pease (1860) name, *Cerithium unilineatum*, a valid synonym of *Cerithium zebrum* Kiener, was combined with *Cerithium boeticum* Pease to form a trinomial. In some museum collections the manuscript name, *Cerithium gouldianum* Pilsbry & Vanatta, is found associated with lots of *Cerithium boeticum*, but the name has no validity.

Discussion: As mentioned above, *Cerithium boeticum* had been condsidered to be synonymous with the common Indo-Pacific species, *Cerithium zebrum* Kiener, but the former species has a thicker, less elongate shell with coarser sculpture, few weak varices, a stronger anterior canal, and a different kind of protoconch than *Cerithium zebrum* (see Figs. 18–26); moreover, *Cerithium boeticum* appears to be restricted to the Hawaiian Islands, whereas *Cerithium zebrum* is distributed throughout the Indo-Pacific. Shells of the two species frequently share similar color patterns, especially among the banded, striped morphs, but when closely compared, they are seen to be really quite different. Radular differences between the two species although slight, are consistent and serve to distinguish each of them (see Table 3). The very thin, nearly transparent operculum of *Cerithium boeticum* (Fig. 25) differs from the thicker one of *Cerithium zebrum*.

Gould (1851) mentioned that *Cerithium boeticum* (cited as *Cerithium pusillum*) was "like *C. ferrugineum* Say, but much smaller". *Cerithium ferrugineum* is a synonym of *Cerithium lutosum* Menke, a small species from the western Atlantic, and indeed *Cerithium boeticum* does bear some resemblance to small morphs of *Cerithium lutosum* in overall shell morphology (see Houbrick, 1974, pl. 41).

An unusual anatomical feature of *Cerithium boeticum* is the large, well-developed bipectinate osphradium. Although *Cerithium zebrum* also has a bipectinate osphradium, the pectins are poorly defined. A bipectinate osphradium is common to all members of *Cerithium* Bruguière and *Clypeomorus* Jousseaume (see Houbrick, 1974, 1985), but not as common among *Bittium* species (pers. obsr.). Although *Cerithium boeticum* has a weakly scalloped operculiferous lobe, the lateral epipodial skirt, indicative of *Bittium* species, is absent. The absence of a spermatophore bursa in the lateral lamina of the pallial oviduct, which is the hallmark of *Bittium* species, is one of the chief anatomical reasons for reassignment of this species to *Cerithium*. However, the specimens studied herein may not have attained complete reproductive maturity, and this needs reconfirmation.

Cerithium boeticum lives in shallow water on subtidal rubble where it is frequently found on marine algae. This species has lecithotrophic development, which is reflected in its relatively unsculptured protoconch, comprising only one whorl with a nearly straight apertural lip (Fig. 26).

Cerithium boeticum appears to be endemic to the Hawaiian Islands. It is geographically sympatric with *Cerithium zebrum*, especially in the northern part of the Hawaiian chain. This species has been recorded from the Pleistocene of Molokai (Ostergaard, 1939, as *Cerithium boeticum*).

Table 3. Characters defining *Cerithium zebrum* and *Cerithium boeticum*.

Cerithium zebrum	*Cerithium boeticum*
Sculpture	
1. Weak axial riblets	Strong axial ribs
2. Many weak spiral beads	Fewer strong spiral beads
3. Weakly impressed suture	Strongly impressed suture
4 Many broad white varices	Few weak varices
5. Protoconch highly sculptured	Protoconch unsculptured
6. Thin outer apertural lip	Thick outer apertural lip
7. Aperture ¼ shell length	Aperture ⅓ shell length
Radula	
1. Radula short	Radula very short
2. Rachidian height equal to width	Rachidian wider than tall
3. Rachidian cusp flanked with 2 denticles on each side	Rachidian cusp flanked with 3 denticles on each side
4. Inner marginal with 3 inner and 2 outer denticles	Inner marginal with 2 inner and one outer denticle
Osphradium	
1. Weakly bipectinate	Large, strongly bipectinate
Development	
1. Plantotrophic	Lecithotrophic

A summary of the differences between these two species is presented below, in Table 3.

CONCLUSIONS

Evidence is presented above to show that the Hawaiian species, *Cerithium boeticum*, is morphologically distinct from *Cerithium zebrum*. Although both species had previously been assigned to *Bittium*, anatomical evidence shows that this is incorrect. As both taxa were thought to be *Bittium* species, they were omitted from my Indo-Pacific *Cerithium* monograph (Houbrick, 1992). *Cerithium boeticum* is restricted to the Hawaiian Islands while *Cerithium zebrum* has a very wide Indo-Pacific distribution, including the Hawaiian Islands.

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Rediscovery of *Turbinella thersites* Reeve, 1847, with Notes on its Taxonomic Position (Gastropoda: Fasciolariidae)

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ABSTRACT

The holotype of *Turbinella thersites* Reeve, 1847, was believed to have been collected in China; no further specimens have subsequently been reported. Comparison with recently trawled material indicates that it was actually dredged on the Agulhas Bank. *Turbinella thersites* is here transferred from the family Turbinellidae to the genus *Fasciolaria*, within the family Fasciolariidae.

Key words: Fasciolariidae; Turbinellidae; South African; neritic; *Fasciolaria*; *Turbinella*.

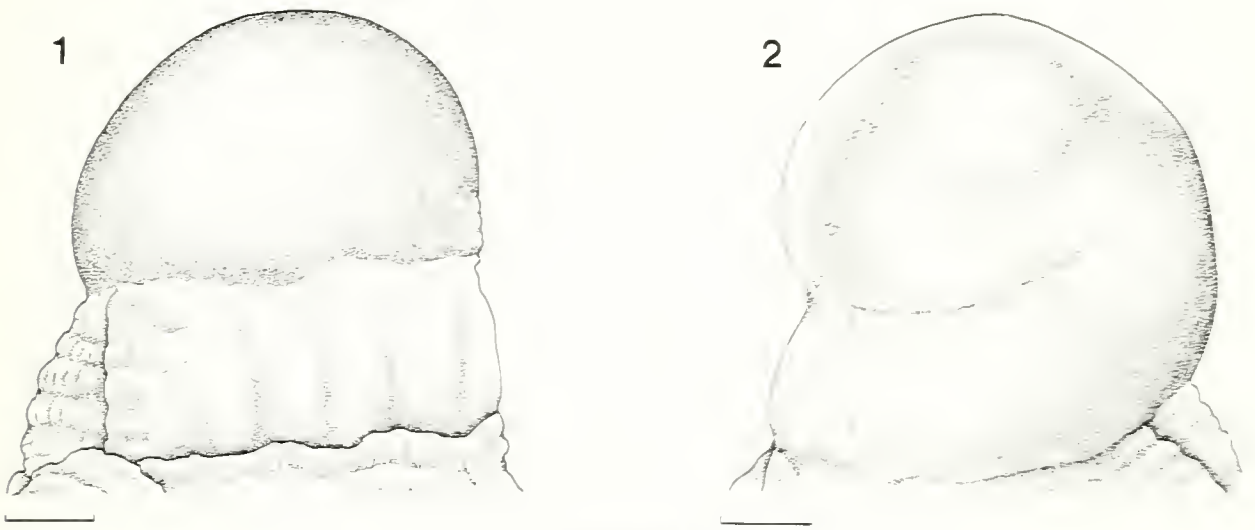
INTRODUCTION

Turbinella thersites Reeve, 1847, was based on a single specimen (Fig. 3) originally in the collection of Captain Sir Edward Belcher, and supposedly from China. Noting that it appeared to be immature, Reeve observed that "it rather partakes of the character of *Fasciolaria*", a view echoed by Melvill (1891), who speculated that it might belong to either *Fasciolaria* Lamarck, 1801 (family Fasciolariidae) or *Tudicla* Röding, 1798 (Turbinellidae). Kobelt (1874) cited it as *Turbinella* (*Plicatella*) *thersites*, and Tryon (1881) similarly included it within the genus *Latirus* Montfort, 1810 (= *Plicatella* Swainson, 1840). Finally, Yen (1942), in a paper on Chinese gastropods in the Natural History Museum, London, published a photograph of the holotype, under the name *Tudicla thersites*, and quoted the type locality without comment. No specimens additional to the holotype are on record, and no further reference to the species has been traced, notwithstanding the considerable body of literature that has been published in recent decades on the mollusks of the Sino-Japanese region.

Among the larger mollusks that are brought up in the nets of commercial trawlers operating on the Agulhas Bank, the continental shelf south of South Africa, are several species of *Fasciolaria*. Most commonly trawled are *F. scholvieni* Strebel, 1912, bathymorphs of *F. lugubris lugubris* Reeve, 1847, and its eastern subspecies *F. lugubris heynemanni* Dunker, 1871, and the bathyal *F. rutila* (Watson, 1882); less commonly seen is *F. wattersae* Kilburn, 1974. On rare occasions a fifth species, distinguishable by its sculpture of auriculate ribs, is trawled. Such ribs similarly characterize the "lost" *Turbinella thersites*, and comparison of juvenile specimens of this "fifth species" with the equally juvenile holotype of *T. thersites* confirms their identity.

At the time of description of *Turbinella thersites*, the only Agulhas Bank mollusks known had been dredged during the cruises of the *H.M.S. Sulphur* (1836–1842) and *H.M.S. Samarang* (1843–1846), both captained by Belcher. Confusion of localities in Belcher material from these voyages is not infrequent, and using the line of reasoning advanced by Tomlin (1925: 310), with regard to the origins of the holotype of *Turritella ferruginea* Reeve, 1849, one can speculate that the holotype of *Turbinella thersites* was originally amongst the mollusks dredged by Belcher on the Agulhas Bank during the voyage of *H.M.S. Samarang* (this expedition was specifically mentioned by Reeve under the description of *Turbinella [= Latirus] belcheri* Reeve, 1847). Indeed the case of *Turritella declivis* Adams & Reeve, 1850, is directly comparable: although originally said to have been dredged by the *Samarang* in the "China Sea", this species was subsequently shown (Tomlin, 1925: 313) to be characteristic of the Agulhas Bank biota. Although at present little precise data is available for *Fasciolaria thersites*, indications are that, like *Turritella declivis*, it is a continental shelf species endemic to the Agulhas Bank.

The second known example (Fig. 5) of *Fasciolaria thersites* was actually collected in 1962, but its identity went unrecognized, until it was sent to me for comment in 1986 by J. H. McLean of the Los Angeles County Museum. Curiously, associated with it was a similar error in localization. Originating from the collection of the late Franz Steiner, the label states: "This shell was found in dredged sand, Nacala, Mozambique, on the 19 June, 1962, by me". Biogeographically, it would be unprecedented for such a temperate-water Agulhas Bank species to live also on the tropical coral coast of northern Mozambique, and its origin is surely adventitious. It is not impossible that this specimen was jettisoned from a ship docking in Nacala harbor, but although worn, it lacks the porcellaneous appearance normally seen in shells that have lain on coral sand for a lengthy period. It is thus



Figures 1–2. Protoconch of *Fasciolaria thersites* Reeve, 1847. Scale lines = 1 mm.

more probable that Steiner accidentally separated it from a sample of trawled Cape mollusks, and mixed it with his Mozambican finds. Indeed, in 1962 or 1963 I was personally told by Steiner (then a radio-operator in the merchant navy) that while on the Nacala route he regularly received trawled shells from a source in Cape Town, who accumulated them in barrels of preservative on his behalf.

This species and its temperate-water South African congeners agree in teleoconch characters with the genus *Fasciolaria* Lamarck, 1799, in its broadest sense. Radula characters, known for all species (Kilburn, 1974; Barnard, 1958), except *F. thersites*, also agree. Although species with shoulder nodules are generally referred to subgenus (sometimes even genus) *Pleuroploca* P. Fischer, 1884, such a classification does not address the problem of taxa such as *Fasciolaria filamentosa* (Röding, 1798) and *F. lugubris* Reeve, 1847, in which nodules are present or absent according to individual or population. The five species endemic to South African waters share a close morphological similarity but differ from all other species of *Fasciolaria* in their extremely large and bulbous protoconch (Figs 1–2), which has a basal diameter of 3.0–3.5 mm, according to species and individual. Such a protoconch cannot be dismissed as merely an adaptive correlation with mode of development, because this is similarly non-planktotrophic in four of the five other species of *Fasciolaria* (= *Pleuroploca*) in which development is known (see D'Asaro, 1970a, 1970b; Gohar & Eisawy, 1967; Shepherd & Thomas, 1989), and is there associated with a much smaller protoconch. A second character of possible significance is egg-capsule shape; in the sole Cape species in which these are known (*F. lugubris*), capsules differ from those reported for other species of *Fasciolaria* in being dorsally rounded without a demarcated escape hatch (see Kilburn & Rippey, 1982: text fig. 62). Egg capsules have been described for three species from North America, and one each from the tropical Indo-Pacific, Mediterranean and southern Australia (references given above, also Bacci, 1947). In all of these, the capsule is flat-topped, with a structural escape hatch dorsally. It is possible that recognition of the South African species-complex at the subgenus level may ultimately prove warranted on grounds of protoconch size and perhaps capsule form.

Fasciolaria thersites (Reeve, 1847), **n. comb.**
Figures 1–7

Turbinella thersites Reeve, 1847: pl. 4, sp. 21; Melvill, 1891: 409. Type locality: China [here emended to Agulhas Bank].
Turbinella (*Plicatella*) *thersites*: Kobelt in Kster & Kobelt, 1874: 71, 157, pl. 28, fig. 1 (after Reeve); Kobelt, 1876: 21.
Latirus thersites: Tryon, 1881: 91, pl. 69, fig. 137 (after Reeve).
Tudicla thersites: Yen, 1942: 237, pl. 25, fig. 178 (holotype).
Fasciolaria wattersae non Kilburn, 1974: Richards, 1981: 63, pl. 35, fig. 300.

Description: Shell fusiform, with bluntly papilliform apex, siphonal canal equal in length to aperture, curved slightly to right, suture moderately shallow, whorls strongly convex, except immediately below suture where they are shallowly concave. Inner lip with a thin callus glaze, smooth except for a thin spiral ridge just above mid-parietal region and three oblique basal pleats, of these the strongest pleat is situated at entrance to siphonal canal, and the weaker posterior two decrease in strength and are scarcely visible from without the aperture. Teleoconch sculptured by strongly prosocline, rather tumid axial ribs, which project at shoulder in a roundedly auriculate manner, in most examples, axials become weak on later whorls, except sometimes for an occasional strong rib, but they may remain strong throughout; fine spiral threads, crossed by microscopic collabral threads, present overall. First teleoconch whorl with 8 straight, prosocline axials, the first few low and relatively close, thereafter in transverse section thick, strongly rounded, slightly

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4
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6
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compressed, more or less equal to intervals, which are flattened; Second whorl with 6–7 axials, third generally with 5, fourth with 4. Spiral lirae unequal in width, groups of fine threads being often separated by groups of coarser ones, those on siphonal rostrum rather uniform in strength. Collabral threads may be pliculate in places, generally rendering intervals between spiral lirae punctiulate and the spirals themselves somewhat scabrous. Off white, with a thin yellowish-brown periostracum. Protoconch bulbous, of about 1½ whorls, first whorl strongly tilted, smooth, last half whorl with uneven, prosocline axial riblets; maximum breadth 3.0–4.8 mm, height 3.1–4.4 mm (ratio breadth/height 0.87–1.13). Maximum dimensions 102.0 × 39.6 mm (R. Le Maitre collection). Holotype (juvenile) 49.0 × 22.1 mm. Operculum oblanceolate with rather obtuse apex, moderately thick with coarse growth lines; color amber-brown, with darker outer edge.

Distribution: Agulhas Bank.

Type material: Holotype in the Natural History Museum, London, accession number 1879.2.26.116, from Lombe-Taylor collection.

Other material examined: Agulhas Bank [Natal Museum (NM) D3482: R. Le Maitre, also several specimens in colln Le Maitre]; off Cape St. Blaize area, *ex pisce* (NM B1087: R. Le Maitre, juvenile); off Storms River mouth, 69 fathoms [= 126 m], in mud, a juvenile shell (NM S4953: C. Marais); same data, 64 fathoms [= 117 m], a broken juvenile (NM S5646: C. Marais); "Nacala harbor, dredged sand", empty shell (NM K1526: F. Steiner, don. J. H. McLean).

Remarks: I have seen no adults of this species with an undamaged lip, and only two specimens (both dead juveniles of about 3 teleoconch whorls) bear a precise locality. Its exact distribution on the Agulhas Bank, both geographic and bathymetric, consequently remains to be established.

Fasciolaria thersites shows much variation in size of protoconch and extent of axial ribbing on the teleoconch; too little material is available to judge whether this reflects geographic, individual or bathymetric variation. The smallest protoconchs measured occur in the holotype and in the specimen purportedly from Nacala (although it is more or less worn in both examples); in the latter individual the axial ribs are unusually strong on later whorls. Similar variability in protoconch size was reported for *F. scholvieni* Strebel, 1912, by Kilburn (1974). In appearance *F. thersites* is most similar to *F. wattersae* Kilburn, 1974, an uncommon species which inhabits the Mossel Bay–Algoa Bay area at depths of about 100–120 m. In *F. wattersae* (Fig. 7) the axial ribs are never auriculate, the spiral sculpture is markedly coarser, and pliculate axial striae are totally absent. Although apparently inhabiting similar depths, *F. thersites* is a much thinner-shelled species. Among the species of *Fasciolaria* endemic to South Africa, the operculum in *F. thersites* is unique in its amber-brown color, this being dark brown in the other species.

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Figures 3–7. *Fasciolaria thersites* (Reeve, 1847) and *F. wattersae* Kilburn, 1974. *Fasciolaria thersites*: **3.** Juvenile holotype of *Turbinella thersites* Reeve, 1847, Natural History Museum, London, 1879.2.26.116, 49.0 ×22.1 mm. **4.** Immature example from Agulhas Bank, 78.9 ×33.6 mm, in R. Le Maitre colln. **5** Specimen supposedly from Nacala Bay, NM K1526, length 76.2 mm. **6** Adult example, Agulhas Bank, depth unknown, NM D3482, length 100,2 mm, outer lip damaged. **7.** *Fasciolaria wattersae* Kilburn, 1974, S. E. of Mossel Bay, 119 m, NM E5898, 98.7 ×32.3 mm.

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The Rediscovery, Morphology, and Identity of *Conus emersoni* Hanna, 1963

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ABSTRACT

Conus emersoni is reported from 310 m off Isla Santa Maria (Floreana), Galapagos Islands, the first record subsequent to its original description. The species is redescribed from eight additional specimens; its operculum, radula, and periostracum are described for the first time. Affinity of the species to *C. teramachii* Kuroda, 1956, is discussed.

Key words: Conidae, *Conus emersoni*, Galapagos Islands, radula.

INTRODUCTION

Subsequent to its description 29 years ago (Hanna, 1963) from two dead, faded and poorly preserved specimens, *Conus emersoni* has remained an enigmatic member of an otherwise extensively studied genus in the Eastern Pacific region. Even as he proposed the species, Hanna (1963) suggested that it might be conspecific with the Indo-West Pacific species *C. australis* Holten, 1802, whereas Walls (1979) placed it as a possible synonym of another Indo-West Pacific species, *C. orbignyi* Audouin, 1831. Keen (1971) treated the species as valid but made no comments on its relationships. Finally, Coomans *et al.* (1986) considered it to be a tentatively valid species but noted that it could be based on fossil material.

Here we report upon eight recently collected specimens from moderately deep water at the Galapagos Islands, two of which are in the collections of the Natural History Museum of Los Angeles County and six in the American Museum of Natural History. All were provided by André and Jacqueline DeRoy, residents of the Galapagos Islands. These specimens extend the distribution from Cabo San Lucas, Baja California Sur, to the Galapagos Islands, Ecuador, and allow a redescription of the species with the first report on the morphology of the radular tooth, the operculum, and the periostracum.

Abbreviations of museums mentioned in the text: AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; LACM, Natural History Museum of Los Angeles County.

SYSTEMATICS

Conus emersoni Hanna, 1963
(figures 1–13)

Conus emersoni Hanna, 1963:25, pl. 1, fig. 2, Walls, 1979:776 [with unnumbered figure of CAS paratype]; Coomans, Moolenbeek & Wils, 1986:114, fig. 718 [holotype, 2 views].
Conus (Asprella) emersoni; Keen, 1971:663, fig. 1497 [holotype].

Diagnosis: Spire scalariform throughout its length, shoulder angle retaining square nodules; sculpture on final whorl of numerous, closely spaced, shallow sulci; posterior notch shallow; whorl tops sculptured by one to two cords that fade in whorl three to be replaced by numerous fine striae.

Description: Shell elongate-conical, whorl sides flat to very slightly convex; shoulder angular. Anterior end not deflected dorsally. Sculpture of numerous (30–50) closely spaced, shallow sulci, most pronounced at anterior end and fading in intensity towards shoulder. Color pattern variable, consisting of three irregularly developed bands, at shoulder, in area just posterior to midbody area, and in area just anterior to midbody. Bands variously interrupted and scalloped, producing reticulate or blotched pattern; bands separated by areas with rows of spiral dashes or longitudinal reticulations. Dashes and reticulations may be quite pronounced (holotype) or lacking (Galapagan specimens). Anterior end marked by spirally elongated blotches or lines. Color markings in fresh specimens medium brown, fading to light brown in dead specimens.

Spire very slightly convex in profile, scalariform throughout and moderately elevated, carinate, carina interrupted by numerous square nodules, 30–40 per whorl; nodules fading in whorl six although carina may remain pronounced. Protoconch unknown (not intact in any of the specimens). One or two spiral cords on first two or three teleoconch whorls, replaced on later whorls by numerous, exceedingly fine striae. Whorl tops colored by variably developed markings, matching those of body whorl, between nodules or crossing entire width of whorl

Figures 1–7. *Conus emersoni* Hanna, 1963. **Figures 1–3.** Type material dredged off Los Frailes, Baja California, depth 549 m. **1.** Holotype, AMNH 105211, length 43.0 mm, faded, dead-collected specimen, lacking periostracum. **2, 3.** Paratype, CAS 12405, length 49.0 mm, subfossil specimen (surface gray), showing naticid bore hole. **Figures 4–7.** Newly reported specimens dredged off Isla Santa Maria (Floreana), Galapagos Islands, Ecuador, depth 310 m. **4.** AMNH 248261, length 46.2 mm, dead-collected specimen **5.** LACM 146906a, length 33.3 mm, live-collected specimen with periostracum intact. This specimen was used for opercular and radular illustration. **6, 7.** LACM 146906b, length 34.0 mm, dead-collected specimen with periostracum removed to show color pattern

top. Whorl tops slightly but distinctly concave in cross section. Posterior notch shallow and C-shaped.

Aperture narrow, white inside except where exterior coloration shows through near lip. Interior constrictions and apertural flanges absent or at least not developed in available specimens.

Periostracum thick, dark brown, markedly pilose both on body and spire. Extremely fine hairlike extensions of periostracum not organized into any obvious pattern. These projections are apparently easily worn off, as they are pronounced on the dorsal side of one live-collected specimen (figure 5) but are not obvious on the ventral side of the same specimen.

Dimensions (see table 1): The known specimens range in length from 23.0 mm to the 49.0 mm length of the paratype (figures 2, 3). The ratio of width to length ranges from 0.43 to 0.50 (table 1). The largest Galapagan specimen (figure 4) is 46.2 mm in length. All specimens have the protoconch eroded, the spire tips filled by secondary shell deposition.

Operculum illustrated in figure 8 is 27% of apertural length, weakly serrate on outer edge.

Radular tooth (figures 9–13) small, 285 μm in length; massive base with pronounced basal spur; waist located on anterior half of tooth, with small spine on posterior border in same plane as basal spur. Tooth opening rather long, extending about one-quarter the length. Tip with small barb opposite short blade.

Distribution: The holotype and one paratype were collected off Los Frailes, Cape San Lucas, Baja California in 550 m (given originally as 300 fathoms by Hanna, 1963). The eight newly discovered specimens were dredged in 310 m (170 fathoms) off Isla Santa Maria (Floreana), Galapagos Islands, 7 May 1979 by André and Jacqueline DeRoy (table 1).

DISCUSSION

The rediscovery of *Conus emersoni* in the Galapagos Islands should put to rest speculation that this species is a synonym of either *Conus australis* (suggested by Hanna, 1963) or *C. orbignyi* (suggested by Walls, 1979). Each of these Indo-Pacific species is unlike *C. emersoni* in having persistent sulci on the body whorl along with persistent cords on the spire whorl tops. *Conus emersoni* differs in having the sulci strong only anteriorly and in having fine spiral striae on the whorl tops. Radular differences are that the radular tooth of *C. orbignyi* has three anterior barbs (Kilburn, 1973: fig. 6), whereas that

Figures 8–13. *Conus emersoni* Hanna, 1963. **8.** Operculum, same specimen as figure 5, length 7.3 mm, nucleus lost. **Figures 9–13.** SEM views of single radular tooth, length 285 μm, from same specimen as in figure 5. SEM photos by H. Chaney. **9.** Oblique anterior view showing apical surface, with pronounced basal spur and small spine on posterior border of waist. **10.** Enlarged view of apical surface, with small barb and enrolled blade. **11–13.** Three lateral views, showing differing axial rotation of tooth.

of *C. emersoni* has but two. The radular tooth of *C. australis* has a serrate shaft along with an enlarged cusp at the posterior end of the row of serrations (A. J. Kohn, radular slide collection); neither feature is present on the radular tooth of *C. emersoni*.

The scalariform spire and color markings of *Conus emersoni* have a superficial resemblance to that of the Panamic species *C. emarginatus* Reeve, 1844 (a species often misidentified as *C. recurvus* Broderip, 1833). Differences are that *C. emarginatus* has a deep posterior notch (rather than shallow notch) and a smooth (rather than pilose) periostracum. The radula of *C. emarginatus* (Nybakken, 1970: fig. 5, as *Conus recurvus*) has three barbs anteriorly, like that of *C. orbignyi*, rather than *C. emersoni*, in which there are two barbs.

The scarcity of *C. emersoni* may be due to the great depth at which it occurs and the paucity of sampling at depths below 300 m.

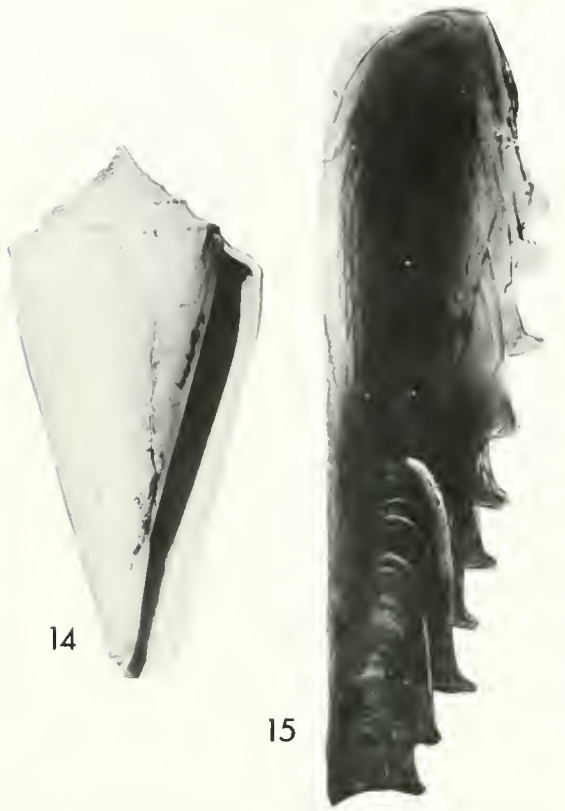
It is possible that the specimens from the Galapagos Islands are specifically or subspecifically distinct. They differ in color pattern (that of the holotype being more intricate) and in spire profile (that of the holotype appearing to be more acute). However, such intraspecific differences in color pattern are not uncommon in *Conus*. In fact, the faintly indicated color pattern of the paratype that shows on the better preserved dorsal surface (figure 3) is more similar to that of the Galapagan specimens (figures 5–7) than to that of the holotype (figure 1). The ground color of the paratype has a gray cast that is suggestive of fossil or subfossil condition. The holotype is in fresher condition, although it retains no periostracum; it shows evidence of growth damage to the shoulder at a stage two whorls above the termination of the lip, which appears to have altered the profile of the final two whorls, resulting in a greater downward slope to the spire and the loss of the nodules in the final two whorls.

The question as to whether the two widely disjunct records represent the same species can only be answered after additional specimens from the vicinity of the type locality become known. It is our opinion, based on the specimens examined, that there is no clear evidence to suggest that the Galapagan specimens are not conspecific with the Mexican specimens.

Conus emersoni is not closely similar to any other eastern Pacific conid. Shell morphology, including the

Table 1. Shell dimensions and proportions of the known specimens of *Conus emersoni* Hanna, 1963.

Specimen	Condition	Length	Width	Width/ length
AMNH 92200 (holotype)	dead	43.0	18.5	0.43
CAS 12405 (paratype)	subfossil	49.0	22.5	0.46
LACM 146906a	live	33.9	17.0	0.50
LACM 146906b	dead	34.0	15.5	0.46
AMNH 248262	live	35.0	15.7	0.45
AMNH 248263	live	31.5	14.3	0.45
AMNH 248261	dead	46.2	22.3	0.48
AMNH 248169a	live	23.0	10.8	0.47
AMNH 248169b	dead	30.0	14.9	0.50
AMNH 248169c	live	26.8	12.8	0.48



Figures 14, 15. *Conus teramachii* Kuroda, 1956. **14.** Specimen with growth scar producing lowered shoulder angle of final whorl, periostracum removed. Off NE coast Taiwan, trawled, depth unknown. LACM 68994, length 79.8 mm. **15.** Operculum with strongly serrate edge, nucleus lost, trawled off Taiwan. Specimen in H. Chaney collection, length 19.1 mm.

shoulder carina with square nodules, is similar to that of *C. teramachii* Kuroda, 1956 (figure 14), a species reported from similar depths off Japan and Taiwan (Kuroda, 1956; Walls, 1979). Our illustrations of the radular tooth of *C. emersoni* (figures 9–13) are comparable to those of Azuma (1961: fig. 11) for *C. teramachii* (as *C. petricosus* Azuma, 1961). In addition, *C. teramachii* also has a strongly serrate operculum (figure 15), much more pronounced than that of *C. emersoni* (figure 8). The character state of the serrate operculum was stressed in the original diagnosis of the subgenus *Profundiconus* Kuroda, 1956—type species *Chelyconus* (*Profundiconus*) *profundorum* Kuroda, 1956 [= *Conus smirna* Bartsch and Rehder, 1943]. The type species of *Profundiconus* also has square nodules on the shoulder carina, but these are apparent only in young stages.

We refrain, however, from further treatment of the subgeneric allocation of the species under discussion because comparison to other available generic level taxa is beyond the scope of this paper. We recognize that a generic level classification of Conidae needs to be based on all the recognized species, including fossils, at a minimum treating characters that include adult and juvenile shell morphology, and, for the living species, the operculum, and radula.

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The Benthic Mollusk Faunas of Two Contrasting Reef Paleosubenvironments: Falmouth Formation (late Pleistocene, Last Interglacial), Jamaica

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ABSTRACT

The last interglacial (about 125,000 years old) raised reefs of the Falmouth Formation of Jamaica contain a diverse fauna of benthic mollusks. Large collections of mollusks have been made from two contrasting reef localities and paleosubenvironments. Calcareous muds of lagoonal origin were well-cemented, biassing collecting towards larger individuals, whereas poorly-cemented sandy sediments of a coral framework were friable and thus amenable to bulk sampling, yielding numerous micromollusks. Identification of over 3,000 bivalve, gastropod and scaphopod specimens shows the molluscan faunas of each environment to be dominated by different species. The coral framework fauna is numerically dominated by the microgastropod *Caecum pulchellum* Stimpson, 1851, other epifaunal gastropods and arks, while *Bulla striata* Bruguière, 1792 and ceriths dominate the lagoonal sediments. Only *Cerithium algicola* C.B. Adams, 1848, forms more than 2% of the fauna at both localities. 17% of the extant species (27% of the common species) of shallow water benthic mollusks (excluding chitons) from Jamaica have been identified from these two localities.

Key words: Late Pleistocene; benthic reef mollusks; Jamaica.

INTRODUCTION

The present paper is a preliminary report of the molluscan faunas from the late Pleistocene (the last interglacial or Sangamonian) Falmouth Formation (125,000 years B.P.) of northern Jamaica. The mollusks of the Falmouth Formation are important for two principal reasons. Firstly, the Neogene and Quaternary fossiliferous deposits of Jamaica contain a diverse fauna of benthic mollusks that have hitherto been largely ignored by systematists. Indeed, only the famous Pliocene Bowden shell bed in southeastern Jamaica (Woodring, 1925, 1928) and the fauna of the Early Pleistocene Manchioneal Formation (Trechmann, 1930) have so far received monographic treatment. This lack of published information does not reflect the true diversity of the mollusk faunas through this interval and may thus prove misleading to workers not familiar with the geology of the island. For example, Petuch (1988:49) considered that there are few exposures of Miocene age preserved within the Caribbean and South American region, and did not include Jamaica in his list of productive sites, yet in a preliminary survey Jung (1972) listed members of 19 genera from the extensive deposits of the Newport Formation (Lower and Middle Miocene) of the island.

Further, molluscan faunas from last interglacial reefs (and other Pleistocene marine environments; Valentine, 1989) can be a valuable adjunct to studies of extant assemblages from the shallow benthos (but see cautionary comments in Johnson, 1960). The Pleistocene raised reefs of the Caribbean region are recognised to include large faunas of fossil mollusks (see, for example, Cerridwen & Jones, 1991). Unlike those of certain other areas (such as Aldabra Atoll; Taylor, 1978), Caribbean mollusk faunas have apparently changed little since the last interglacial (Petuch, 1988:119), an observation that may have important implications for the study of faunal associations in Recent reefs and associated environments. Mollusk faunas in various biofacies within Pleistocene raised reefs are generally easy to sample, outcropping adjacent to the coast on many Caribbean islands, thus permitting large collections to be made for systematic and paleoecological analysis.

Geology and geological nomenclature: The Falmouth Formation in the Discovery Bay-Rio Bueno Harbour region of Jamaica's northern coast (figures 1-3) rests unconformably on the dolomitized Plio-Pleistocene reef (Land, 1991) of the Hopegate Formation. Lithofacies

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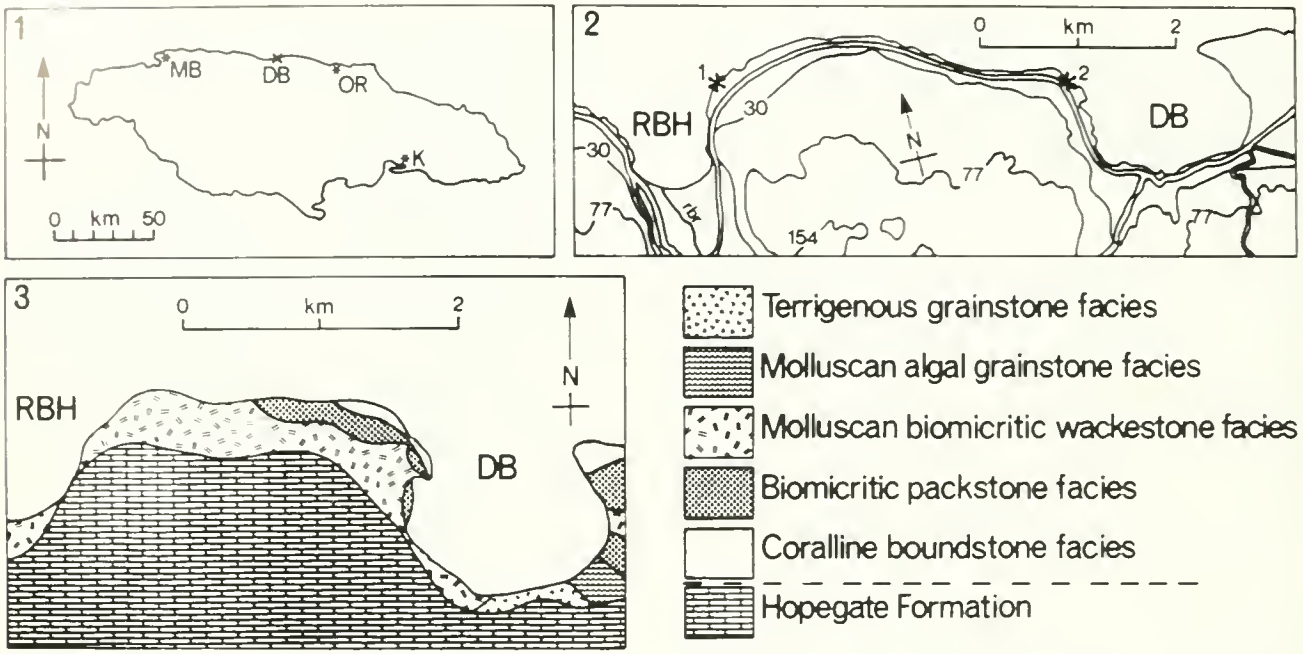


Figures 1–3. Maps of study areas. **1** Outline map of Jamaica, showing the location of the Discovery Bay (DB) region with respect to Kingston (K), Montego Bay (MB) and Ocho Rios (OR). **2**. Topographic map of the Discovery Bay-Rio Bueno Harbour (RBH) area, showing the positions of localities 1 and 2. Contours in m. **3** Geological map of the Discovery Bay-Rio Bueno Harbour area (redrawn after Larson, 1983, figure 6), showing the relative distributions of the major sedimentary facies of the Falmouth Formation in relation to the underlying Hopegate Formation (key right).

within the Falmouth Formation reef (Larson, 1983) contain associated distinct faunal assemblages which have been recognised from the evidence of corals (Larson, 1983; Liddell *et al.*, 1984) and echinoids (Gordon & Donovan, 1992).

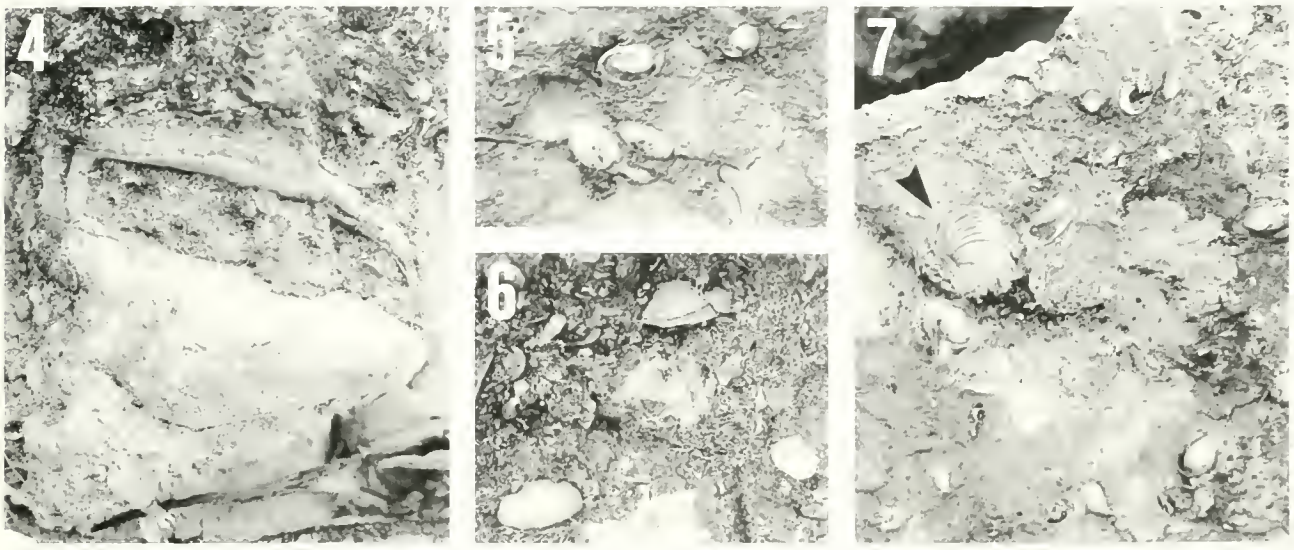
History of research: Hill (1899) named the Falmouth Formation, and recognized the essential elements of the mollusk fauna to comprise *Lucina*, *Cardium*, *Arca*, *Solen* and *Bulla*. Hill (1899, 155) considered this fauna to be worthy of careful study by paleontologists, an invitation that has not been taken up in over 90 years. Robinson (1958) noted *Arca* spp. from the elevated reef at east Rio Bueno Harbour (locality 1 herein), and *Chione cancellata* (Linnaeus, 1767) and *Bulla* cf. *striata* Bruguière, 1792, from the lagoonal facies east and west of Falmouth, Parish of Trelawny (probably lithologically similar to locality 2 herein). In 1960, Robinson considered the Falmouth Formation in the Parish of St. Ann to include the mollusks *Lucina*, *Codakia*, *Chione* and *Bulla*, and later commented that this rich fauna is identical with the living fauna of the Jamaican coastal waters (Robinson, 1963:52). Recent studies of the fossil scaphopods of Jamaica (Donovan and Littlewood, 1989; Donovan, 1990) have recognised *Dentalium* sp. cf. *D.* (*Antalis*) *antillarum* d'Orbigny, 1842, and *D.* (*Graptacme*) *semistriolatum* Guilding, 1834, from the east Rio Bueno Harbour locality.

The specimens discussed herein are deposited in the Department of Palaeontology, British Museum (Natural History). For uncertainties in our taxonomic assignments (particularly for poorly preserved or fragmentary specimens), we have used question marks thus: *Agenus ?species* signifies that we are uncertain of the specific assignation; *?Agenus aspecies* indicates that some doubt exists concerning the generic (and, thus, also specific) assignment. This differs in detail, but not in spirit, from the recommendations of Bengston (1988).

MATERIALS AND METHODS

The Falmouth Formation of the Discovery Bay-Rio Bueno Harbour area has been subdivided into five principal reefal subenvironments by Larson (1983; figure 3 herein). Large collections of benthic mollusks were made from two contrasting paleosubenvironments (localities 1 and 2, described below) within this continuum. These particular subenvironments and localities were chosen because of their large mollusk faunas and easy access. The mollusk collections from each locality were made over a period of 22 months, from April 1988 until February 1990. Both collections are time-averaged, having been collected from float, the rock face and as bulk samples from throughout 2-4 m of section in each case, as bedding planes and other obvious time marker horizons are not apparent. However, the value of collecting mollusks from discrete beds (even when preserved within reefs is debatable, as at any one time the fauna will include shallow and deep infaunal, sediment surface epifaunal, and (in the case of the three-dimensional coral framework at locality 1) epifaunal taxa living well above the soft sediment surface.

Specimens collected in the field were generally at least



Figures 4–7 Field photographs of mollusks of the Falmouth Formation. **4**. *Strombus gigas* Linnaeus, 1758, at locality 1; 0.3 ×. **5–7**. Locality 2. **5** Mainly *Bulla striata* Bruguière, 1792; 0.6 × **6** General view of weathered surface showing abundant (mainly molluscan) shell hash; 0.6 ×. **7** Mainly *Bulla striata* Bruguière, 1792, associated with an articulated shell (arrowed) of *Chione paphia* (Linnaeus, 1767); 0.4 ×.

5 mm in maximum dimension and even shells of this size were easily overlooked without repeated scanning of a limited area at a time. It proved much easier to detect small specimens during laboratory analysis using a Wild binocular microscope. Preliminary field identifications were checked in the laboratory using standard taxonomic references, including Abbott (1954, 1958, 1974), de Jong and Coomans (1988), Fisher (1988), Humfrey (1975), Morris (1987), Vaught (1989), and Warmke and Abbott (1961). Total numbers of whole shells and (for bivalves) disarticulated valves are tabulated. Whole shell equivalents (discussed in Cerridwen and Jones, 1991) were used in calculating relative proportions of mollusks for graphical analysis.

Locality 1

(Locality 7 of Liddell *et al.*, 1984; locality 3 of Donovan & Gordon, 1989). East side of Rio Bueno Harbour, Parish of St. Ann, with the Falmouth Formation exposed as a line of low cliffs (GR 394 572). At this locality the unconformable contact with the underlying, dolomitised Hope Gate Formation (figure 3) formed the hard substrate for Falmouth Formation reef growth. Previous interpretations have considered this locality to represent either a patch reef in the back reef lagoon within the molluscan biomicritic wackestone facies *sensu lato* (Larson, 1983; figure 3 herein) or perhaps part of the shallow fore reef (Robinson, 1958; Liddell *et al.*, 1984).

Mollusk-rich sediments at this locality occur beneath an altered caliche cap (Land & Epstein, 1970) in a framework of shallow-water corals, particularly *Porites* spp. and *Acropora* spp. (Liddell *et al.*, 1984: 77). The matrix between corals is a friable, weakly-cemented carbonate sand which includes a diverse benthic fauna, including echinoid (Gordon & Donovan, 1992) and ophiuroid (Donovan *et al.*, in press) ossicles, crabs (Morris, in press), disarticulated chiton valves (Donovan *et al.*, research in progress), scaphopods (Donovan & Littlewood, 1989; Donovan, 1990), gastropods and bivalves. Due to the friable nature of the sediment, two collecting methods were used. Firstly, mollusk specimens that were weathering out of the exposed face (figure 4) were removed manually. The fauna collected by this method was dominated by bivalves and gastropods, with three scaphopod shells. Secondly, bulk samples were collected by the bagful. In the laboratory these samples were emptied into shallow trays, dried in an oven overnight, then washed through a nest of sieves using cold water and redried. Sieved aliquots were then picked by eye (coarse fractions) or under the binocular microscope (fine fractions: fractions finer than coarse sand were not picked). The fauna collected by this method was dominated by bivalves, gastropods and (in the finer fractions examined) chiton valves, but no further scaphopods were found. A total of 1669 benthic mollusks (excluding chiton valves; Donovan *et al.*, research in progress) have been identified from this locality (table 1).

Locality 2

(Locality 5 of Liddell *et al.*, 1984). This is an outcrop of hard, fine-grained, well-lithified, but occasionally chalky, limestone exposed along the shoreline as a low terrace east of the Discovery Bay Marine Laboratory, Parish of St. Ann (GR 405 569). This lithology has been interpreted as having been formed in a back reef environment (Liddell *et al.*, 1984:76), presumably a lagoon, forming part of the molluscan biomicritic wackestone facies *sensu strieto* of Larson (1983; figure 3 herein).

Table 1. Mollusk fauna collected from locality 1, east of Rio Bueno Harbour. Key: * = includes 11 juveniles, plus 2 shells not collected; ** = with apparent growth deformity; + = valve incomplete; ++ = probably mostly *Arca imbricata* Bruguière; S = shells or identifiable shell fragments; V = valves; LV = left valve; RV = right valve; O = operculum; J = juvenile shells.

Gastropods	
Diodora listeri (d'Orbigny, 1853)	25S
Diodora ?cayenensis (Lamarck, 1822)	12S
Diodora ?minuta (Lamarck, 1822)	1S
Fissurella barbadensis (Gmelin, 1791)	1S
Acmaea ?antillarum (Sowerby, 1831)	1S
Acmaea pustulata (Hellbling, 1779)	60S
Cittarium pica (Linnaeus, 1758)	3S
Tegula fasciata (Born, 1778)	3S
Astraea ?caelata (Gmelin, 1791)	1O
Astraea tecta (Solander, 1786)	4S
Nerita versicolor Gmelin, 1791	1S
Nerita tessellata Gmelin, 1791	2S
Nerita sp. indet.	1S
Neritina virginea (Linnaeus, 1758)	1S
Neritina punctulata Lamarck, 1816	2S
Littorina ?nebulosa Lamarck, 1822	2S
Alvania ?aberrans C. B. Adams, 1850	1S
Heliacus infundibuliformis (Gmelin, 1791)	1S
Petaloconchus irregularis (d'Orbigny, 1842)	2S
Petaloconchus erectus Dall, 1888	1S
Petaloconchus mcgintyi Olsson and Harbison, 1953	2S
Serpulorbis decussata (Gmelin, 1791)	5S
Serpulorbis ?decussata (Gmelin, 1791)	1S
Serpulorbis ?riisei (Mörch, 1862)	1S
Caecum ?insularum Moore, 1970	1S
Caecum plicatum Carpenter, 1858	1S
Caecum pulchellum Stimpson, 1851	657S
Modulus modulus (Linnaeus, 1758)	13S
Cerithium ?litteratum (Born, 1778)	7S
Cerithium guinaicum Philippi, 1849	3S
Cerithium ?eburneum Bruguière, 1792	2S
Cerithium algicola C. B. Adams, 1848	92S
Cerithium sp.	3S
Cerithium sp. indet.	3S
Hipponix antiquatus (Linnaeus, 1767)	33S
Strombus gigas Linnaeus, 1758	*36S
Cypraea zebra Linnaeus, 1758	1J
Cypraea cinerea Gmelin, 1791	2S
Polinices lacteus (Guilding, 1834)	9S
Morum oniscus (Linnaeus, 1767)	3S
Cymatium 'pileare' (Linnaeus, 1767)	1J
?Cymatium nicobaricum (Röding, 1798)	1J
Cymatium ?parthenopeum (von Salis, 1793)	5S
Cymatium sp. *sensu lato*	1J
?Cymatium sp.	1J
Bursa cubaniana (d'Orbigny, 1842)	1J
Columbella mercatoria (Linnaeus, 1758)	81S
Engoniophos ?unicinctus (Say, 1826)	1S
?Melongena melongena (Linnaeus, 1881)	2S
Fasciolaria tulipa (Linnaeus, 1758)	2S
Latirus ?brevicaudatus Reeve, 1847	1S
Leucozonia nassa (Gmelin, 1791)	17S
Mitra barbadensis (Gmelin, 1791)	6S
Hyalina avena (Kiener, 1834)	1S
Conus sp. or spp.	3S
?Mangelia quadrilineata (C. B. Adams, 1850)	2S
Bulla striata Bruguière, 1792	2S
Odostomia sp. or *Pyramidella* sp.	1S
Cheilia equestris (Linnaeus, 1758)	1S
Total	1,130

Table 1. Continued

Bivalves				
Arca ?zebra Swainson, 1883		4LV		
Arca imbricata Bruguière, 1789		77LV	61RV	19S
Barbatia candida (Helbling, 1779)		25LV	37RV	
Barbatia ?cancellaria (Lamarck, 1819)		1LV	4RV	1S
Barbatia tenera (C. B. Adams, 1845)		36LV	24RV	1S
Anadara sp.		1LV		
Arks indet. + +	9V+	32LV	29RV	2S
Brachidontes exustus (Linnaeus, 1758)		4LV		
Smooth ?*Botula fusca* (Gmelin, 1791)				1S
Lithophaga ?nigra (d'Orbigny, 1842)				1S
Isognomon ?alatus (Gmelin, 1791)		1LV	2RV	
Isognomon radiatus (Anton, 1839)		10LV		
Isognomon sp. indet	1V+			
Lima scabra (Born, 1778)	1V+	4LV	5RV	
Ostreola equestris Say, 1834		1LV		
Codakia orbicularis (Linnaeus, 1758)			2RV	
Codakia ?orbiculata (Montagu, 1808)		2LV	1RV	
?*Codakia* sp.		1LV		
Chama macerophylla Gmelin, 1791		9LV	13RV	3S
Chama ?macerophylla Gmelin, 1791		4LV	6RV	
Pseudochama radians (Lamarck, 1819)			1RV	
Americardia media (Linnaeus, 1758)			1RV	
Americardia guppyi (Thiele, 1910)		1LV		
Chione cancellata (Linnaeus, 1767)		1LV	1RV	
Periglypta listeri (Gray, 1838)			1RV	
Tellina listeri Röding, 1798		1LV		
Tellina sp. cf. *Tellina ?mera* Say, 1834		2LV		
Tellins indet	1V+	2LV	5RV	
Tellinacean sp. indet. A		1LV		
Tellinacean sp. indet. B		3LV	1RV	
?Tellinacean sp. indet.**			1RV	
Arcopagia fausta (Pulteney, 1799)		28LV	35RV	6S
?*Macoma pseudomera* Dall and Simpson, 1901			1RV	
?*Macoma* sp.			1RV	
?Lucinid or ?pectinacean indet.	1V+			
?Mactracean indet.		2LV	1RV	
?*Periploma papyratium* Say, 1822			1RV	
Bivalve sp. indet			1RV	
Totals			502V	33S
Scaphopods				
Dentalium sp. cf. *Dentalium* (*Anatalis*) *antillarum* d'Orbigny, 1842				1S
Dentalium (*Graptacme*) *semistriolatum* Guilding, 1834				2S
Total				3S

Because of the well-lithified nature of much of this limestone, it was necessary to use a hammer and chisel to remove all specimens seen in the exposed faces (figures 5-7). Specimens were not apparent on all surfaces due to the vagaries of weathering, although breaking open many of these 'unfossiliferous' exposures showed that mollusks were nevertheless common. As well as collecting individual specimens in the field, large fossiliferous slabs containing dense accumulations of mollusks were taken back to the laboratory for mechanical breakdown. A total of 1365 benthic mollusks have been identified from this locality (table 2), including abundant gastropods and bivalves, rare scaphopods, but no chitons.

RESULTS AND DISCUSSION

Taxonomy: Taxa, and number of specimens of each species, from localities 1 and 2 are tabulated in tables 1 and 2, respectively. It is readily apparent that both faunas, although approximately contemporaneous and separated by a distance of only about 3 km, show considerable taxonomic divergence (figures 8, 9). Locality 1 has the more diverse fauna, which is dominated numerically by the micromollusk *Caecum pulchellum* Stimpson, 1851, arks and epifaunal gastropods (although *C. pulchellum* made only a minute contribution to biomass), whereas locality 2 is typified by the occurrence of abun-

Table 2. Mollusk fauna collected from locality 2, east of Discovery Bay Marine Laboratory. Key: * = encrusting *Cerithium algicola* C. B. Adams, 1848, otherwise as for Table 1

Gastropods				
Diodora ?*cayenensis* (Lamarck, 1822)				2S
Turbo canaliculatus Hermann, 1781				1S
Tricolia sp. or spp.				6S
?*Smaragdia viridis viridemaris* Maury, 1917				1S
Rissoina aberans (C. B. Adams, 1850)				1S
?*Rissoina* sp.				1S
Planaxis lineatus (da Costa, 1778)				1S
Modulus carchedonius (Lamarck, 1822)				7S
Modulus modulus (Linnaeus, 1758)				1S
Cerithium algicola C. B. Adams, 1848				101S
Cerithium eburneum Bruguière, 1792				3S
Cerithium litteratum Born, 1778				33S
Cerithium spp. indet. (fragments)				56S
Janthina sp.				1S
?*Niso portoricensis* Dall and Simpson, 1901				3S
Strombus gigas Linnaeus, 1758				17S
Polinices lacteus (Guilding, 1834)				78S
Natica canrena (Linnaeus, 1758)				1S
Naticid sp. indet.				1J
Cymatium ?*caribbaeum* Clench and Turner, 1957				1S
Cymatium muricinum (Röding, 1798)				1S
Cymatium sp. indet. A				1S
Cymatium sp. indet. B				1S
Cymatium sp. indet. C				1J
?*Thais deltoidea* (Lamarck, 1822)				1S
Columbella mercatoria (Linnaeus, 1758)				5S
Anachis obesa (C. B. Adams, 1845)				1S
Anachis ?*pretri* (Duclos, 1846)				1S
Anachis sp. indet.				2S
Nassarius albus (Say, 1826)				1S
Fasciolaria tulipa (Linnaeus, 1758)				2S
Olivella dealbata (Reeve, 1850)				37S
Prunum guttatum (Dillwyn, 1817)				13S
?*Volvarina gracilis* (C. B. Adams, 1851)				1S
Conus ?*centurio* Born, 1778				9S
Conus verrucosus Hwass, 1792				1S
?*Crassispira* sp. indet.				1S
Bulla striata Bruguière, 1792				611S
Retusa candei (d'Orbigny, 1841)				1S
Total				1,00S
Bivalves				
??*Nuculid* sp. indet.		1LV	3RV	
Arca imbricata Bruguière, 1789		1LV	1RV	
Barbatia cancellaria (Lamarck, 1819)		2LV	1RV	
Ark indet. sp.		1LV		
Brachidontes citrinus (Röding, 1798)			1RV	
?*Isognomon* sp.		1LV		
Pinna carnea Gmelin, 1791	1V +			
Pecten ?*chazaliei* Dautzenberg, 1900		1LV?	1RV?	
?*Diplodonta punctata* (Say, 1822)		1LV		
Lucina sp. indet. A		2LV	1RV	
Lucinid sp. indet. A		2LV	3RV	
Lucinids spp. indet.		3LV	3RV	
?*Anodontia alba* Link, 1807		2LV		1S
Codakia costata (d'Orbigny, 1842)		4LV	3RV	
Codakia orbicularis (Linnaeus, 1758)			2RV	
Codakia orbiculata (Montague, 1808)		2LV	2RV	
Divaricella quadrisulcata (d'Orbigny, 1842)		42LV	34RV	
Chama macerophylla Gmelin, 1791			1RV	
Chama sp.	*	2LV		

Table 2. Continued

?Trachycardium sp	1V+			
Americardia guppyi (Thiele, 1910)		2LV	2RV	
Americardia media (Linnaeus, 1758)		1LV	2RV	
Laevicardium laevigatum (Linnaeus, 1758)		6LV	7RV	5S
?Laevicardium laevigatum (Linnaeus, 1758)		3LV	1RV?	
Laevicardium ?sybariticum Dall, 1886	1V+			
Chione cancellata (Linnaeus, 1767)		10LV	11RV	1S
Chione granulata (Gmelin, 1791)			1RV	
Chione paphia (Linnaeus, 1767)		2LV	2RV	2S
Transennella ?conradina Dall, 1883		6LV	2RV	
Transennella ?cubaniana (d'Orbigny, 1842)		2LV	2RV	
Pitar albida (Gmelin, 1791)		13LV	12RV	6S
Tellina alternata Say, 1822		2LV	2RV	
Tellina listeri Röding, 1798	2V+	3LV	2RV	2S
Tellina similis Sowerby, 1806		18LV	10RV	
Tellina sp. indet	4V+	7LV	3RV	
Apolymetis intastriata (Say, 1826)		1LV		6S
Tagelus divisus (Spengler, 1794)		30LV	29RV	2S
Mactra fragilis Gmelin, 1791			2RV	
Totals			325V	25S
Scaphopods				
Cadulus sp.				1S
Dentalium ?antillarum d'Orbigny, 1846				2S
Dentalium sp. (smooth-shelled)				1S
Total				4S

dant *Bulla striata* Bruguière, 1792 and *Cerithium* spp. with other gastropods and rarer bivalves.

Paleoecology and preservation Taxonomic differences are interpreted as being related to paleoenvironmental control. Locality 1 included abundant hard substrates for the attachment of epifaunal bivalves, provided by the coral framework, as well as a sandy substrate suitable for a variety of infaunal and epifaunal taxa. Chitons, which generally prefer a hard substrate, are also common at this locality. In contrast, locality 2 lacks any evidence of a three-dimensional framework structure; indeed, corals were small and isolated in this paleoenvironment. Consequently, epifaunal species are rare and the fauna is dominated by infaunal taxa, particularly *B. striata*, but also including various burrowing bivalves (habitat preferences of many of the groups tabulated herein are summarized in Cerridwen & Jones, 1991: table 3). The only species which forms greater than 2% of both faunas is *Cerithium algicola* C.B. Adams, 1845 (figures 8, 9; tables 1, 2).

Table 3. A comparison of the taxonomic diversity of the extant Jamaican molluscan fauna with nominal species identified herein from the Falmouth Formation. Key: + = after Humfrey (1975); * = excluding rare species; 1, 2 = localities

	Extant+	1	2	1 + 2	%
Scaphopods	11	2	3	4	36
Gastropods	324*	55	37	80	25
	558	55	37	80	14
Bivalves	163*	33	34	56	34
	246	33	34	56	23
Totals	514*			140	27
	831			140	17

The difference in diversity between the localities may be real, although it is almost certainly at least part artifact. This is because of the differing degrees of lithification (and, hence, availability of specimens) seen between the two collecting sites. All specimens from bulk samples from locality 1 were theoretically collected by sieving and picking. In contrast, limestones from locality 2 were not amenable to such processing, being well-lithified, and liberation of specimens was essentially a destructive process. In addition to those specimens broken from the rock, there were some mollusks, particularly those with a fragile shell, that were too easily lost due to breakage while others were being removed. Further, many specimens were probably never seen because they were enclosed within the remaining small chips of rock that were not broken down further. Micromollusks are a common component of the fauna from locality 1, mainly recognized during microscopic examination of the sand-sized sieve fraction. Such a technique is not generally possible with the sediment from locality 2 and, even if detected, small shells are difficult to extract and clean from the hard matrix. The total absence of chiton valves or *Caecum* shells from locality 2 may be real, but the limited diversity of micromollusks from this site suggests that preservational and collecting biases were important factors (in particular, extant *Caecum* is a common component of seagrass communities which presumably occurred in the paleolagoon). Thus, micromollusks were part of the easily collectable fauna only

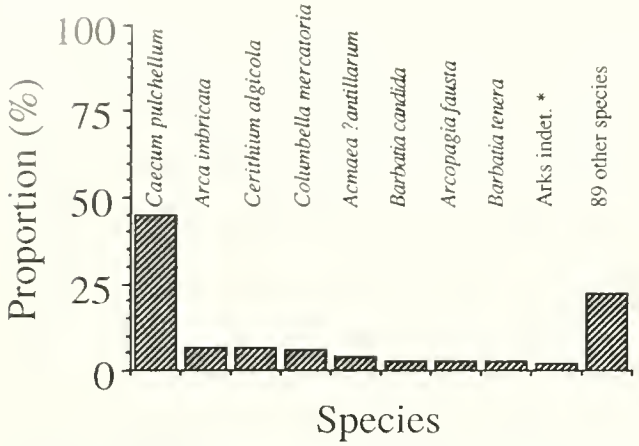


Figure 8. Histogram of relative abundance of mollusk species of locality 1 (n = 1467; bivalves recalculated as whole shell equivalents). 89 species are each present as less than 2% of the total mollusk fauna. * = broken fragments of arks which are too poorly preserved for even generic identification, but which are probably dominantly *A. imbricata*.

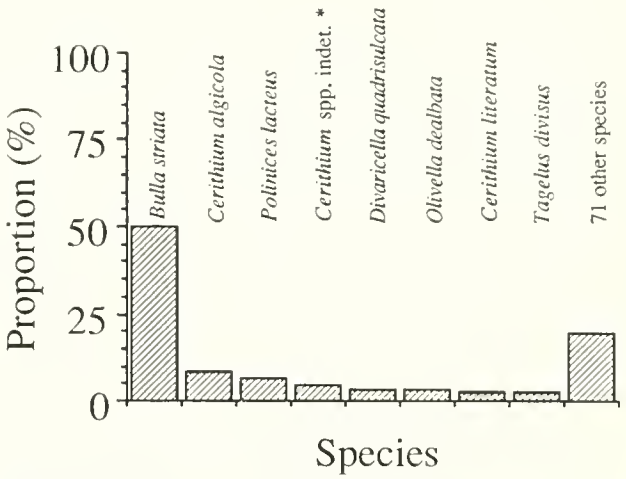


Figure 9. Histogram of relative abundancies of mollusk species at locality 2 (n = 1226; bivalves recalculated as whole shell equivalents). 71 species are each present as less than 2% of the total mollusk fauna. * = broken fragments of dominantly, or entirely, *C. algicola* + *C. literatum* which are too poorly preserved for identification below the generic level.

at locality 1, although it was still possible to extract some small shells from the limestones at locality 2 (particularly robust shells such as *Cadulus* sp. and *B. striata* juveniles).

Macromollusks from both sections are often exquisitely preserved. Whilst bivalves are normally (and chitons invariably) disarticulated, valves often have a highly glossy appearance, such as *Laevicardium laevigatum* (Linnaeus, 1758) at locality 2 and *Polinices lacteus* (Guilding, 1834) at both localities, equivalent to that of fresh shells. Further, shell coloration and/or color banding is preserved in, for example, at least some specimens of *Leucozonia nassa* (Gmelin, 1791) from locality 1 and *B. striata* from locality 2. This indicates that the diagenetic effects leading to the lithification of the limestones (particularly at locality 2) have so far had little influence on the organic molecules that are largely responsible for coloration. However, many shells are poorly preserved, often being corroded and/or abraded. Many show the influence of pre- and post-mortem boring. Pre-mortem borings by predatory gastropods (?*P. lacteus*) have been noted in, for example, *Brachidontes exustus* (Linnaeus, 1758) and *D.* sp. cf. *D.* (*A.*) *antillarum* (see Donovan & Littlewood, 1989) from locality 1. Presumably post-mortem borings produced by ?clionid sponges are common in arks from the same site, while *B. striata* and *P. lacteus* from locality 2 were occasionally bored by polychaetes.

Table 4. Comparison of the extant shallow-water molluscan fauna of Yucatan (Ekdale, 1974) with that of the Pleistocene Falmouth Formation. Key: * = excluding chitons; 1, 2 = localities.

	Species in common with			
	1	2	1 + 2	1 + 2 (%)
Rocky intertidal zone (14 sp.*)	3	1	3	21
Lagoonal and mangrove-associated environments (27 sp.)	9	9	11	41
Broad, shallow backreef (23 sp.)	7	10	10	43
High-energy environment (8 sp.)	1	1	1	13
Open sea assemblage (15 sp.)	4	3	4	27
Cosmopolitan taxa (9 sp.)	2	4	4	44

Comparisons with extant faunas: 17% of the extant, shallow-water, benthic mollusks known from the island at the present day have been identified from localities 1 and 2 (table 3). If the rarer taxa listed by Humfrey (1975) are ignored, this figure rises to 27% (table 3).

Parsons and Brett (1991) have highlighted the fluctuating taxonomic compositions of many tropical, shallow shelf mollusk faunas. The assemblages described from the Falmouth Formation undoubtedly include mollusks from a number of ephemeral communities, having been collected from about 2-4 m of section. While the broad environmental signals of the two facies are obviously different, it is uncertain how the interplay of changing community structure at both sites lead to the preservation of the fossil faunas. Comparisons that we have made between our Falmouth Formation mollusk assemblages and published descriptions of Caribbean shallow-water mollusk communities have been inconclusive, showing no obvious close parallels. As an example, table 4 compares the Falmouth Formation molluscs with the modern shallow-water fauna of northeast Yucatan (Ekdale, 1974). There is no assemblage which shows even a 50% similarity to localities 1+2 combined. Faunal lists of the modern mollusc faunas from particular habitats in Jamaica have not been published (Dr. J.D. Woodley, personal comunication).

CONCLUSIONS

140 nominal species have been identified from the late Pleistocene Falmouth Formation of Jamaica. If rarities

in the extant fauna are ignored, this represents over 25% of the common living species from the island. However, the Falmouth Formation is an averaged sample from a number of ephemeral communities and comparisons with extant Caribbean faunas from similar environments are inconclusive. This preliminary survey highlights the diversity of the mollusk fauna across reef environments and suggests that fossil reefs may be considered as important sampling points during the reconstruction of ancient regional biotas.

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The Systematic Position of the Genus *Nucella* (Prosobranchia: Muricidae: Ocenebrinae)

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ABSTRACT

The muricid genus *Nucella* Röding, 1798 has commonly been placed in Thaidinae Jousseaume, 1888 (Prosobranchia: Muricidae). The Thaidinae (*sensu* Kool, 1989) is monophyletic with and thus synonymous with Rapaninae Gray, 1853 (Kool, 1993, in press). Comparative anatomical investigations of the type species of *Nucella* Röding, 1798 (*Buccinum filosum* Gmelin, 1791 [=*Nucella lapillus* (Linnaeus, 1758)]) and of *Thais* Röding, 1798 (*Murex fucus* Gmelin, 1791 [=*Thais nodosa* (Linnaeus, 1758)]) as well as other rapanines have revealed that inclusion of *Nucella* in Rapaninae would result in polyphyletic groups (Kool, 1989; 1993, in press). Studies of the anatomy, radula, protoconch, shell ultrastructure, and operculum of the type species of *Nucella*, *Ocenebra* Gray, 1847 (*Murex erinaceus* Linnaeus, 1758 [=*Ocenebra erinacea*]) (Ocenebrinae Cossmann, 1903), and *Trophon* Montfort, 1810 (*Murex magellanicus* Gmelin, 1791 [=*Trophon geversianus* (Pallas, 1774)]) (Trophoninae Cossmann, 1903), indicate that *Nucella* has close affinities with Ocenebrinae and Trophoninae. Based on cladistic analyses, it is here proposed that *Nucella* be placed in Ocenebrinae. Results further reveal that the distinctions between Ocenebrinae and Trophoninae are less clear than previously accepted.

Key words: *Nucella*; Ocenebrinae; phylogeny; systematics; comparative anatomy.

INTRODUCTION

The Thaidinae of authors, also referred to as Thaididae, Purpurinae/dae Swainson, 1840, Drupinae Wenz, 1941, etc., has been shown to be a conglomerate of disparate taxa (Kool, 1989; 1993, in press). The taxonomic coherence of the Thaidinae and the boundaries of its genera were based primarily on external shell characters, which are often convergent, obscuring phylogenetic relationships.

Rigorous cladistic analyses based primarily on characters derived from anatomy, radula, operculum, and shell ultrastructure, have shown that para- and polyphyly were wide-spread in the Thaidinae/dae of authors (Kool, 1989). Subsequent phylogenetic studies have revealed that the genus *Rapana* Schumacher, 1817, and the Thaidinae (*in partem*) constitute a monophyletic group, making Thaidinae a junior subjective synonym of Rapaninae (Kool, 1993, in press). The name Rapaninae will herein be used for the clade that includes *Rapana* and *Thais*.

Several species of the genus *Nucella* have been used extensively in ecological studies (Colton, 1922; Crothers, 1983, 1985; Emlen, 1966; Etter, 1987; Kincaid, 1957; Moore, 1936, 1938; Palmer, 1983, 1985; Spight, 1972, 1976). In most of these studies *Nucella* was regarded as a subgenus or synonym of *Thais*. Anatomical studies (Kool, 1986, 1989) of the type species of *Nucella* [*Buccinum filosum* = *Nucella lapillus* (see Kool & Boss, 1992)] and *Thais* [*Murex fucus* = *Thais nodosa*] revealed major differences between these genera. Kool (1988) therefore excluded *Nucella* from the Thaidinae and tentatively placed *Nucella* in the Ocenebrinae (Kool, 1989) on the basis of radular (Sabelli & Tommasini, 1987; Bandel, 1977) and protoconch (Bandel, 1975) morphology as well as anatomical descriptions (Graham, 1941) of *Ocenebra erinacea*.

Although the anatomy of *Nucella lapillus* is well known (Fretter & Graham, 1962; Kool, 1986, 1989; Oehlmann *et al.*, 1988), relatively little is known about the soft parts of *Ocenebra erinacea*. Aspects of the anatomy of *Trophon geversianus* were described by Harasewych (1984), who suggested that similarities (e.g. radular morphology) between members of *Trophon* and *Nucella* may be due either to convergence resulting from similar environmental conditions or to phylogenetic affinity.

The object of this study is to discern the phylogenetic affinities among *Nucella*, *Trophon* and *Ocenebra*.

MATERIALS AND METHODS

The following specimens were used for anatomical studies:

Nucella lapillus; Kittery, Maine, U.S.A. (USNM 857053) (7 ♀, 5 ♂).

Trophon geversianus; Daniel Este, Isla Grande, Tierra del Fuego, Chile (LACM 86-270.2); Puerto Basil Hall,

Table 1. List of characters and character states for *Muricanthus*, *Thais*, *Trophon*, *Nucella*, and *Ocenebra*.

Character	Mur	Tha	Tro	Nuc	Oce
1. Protoconch whorls	0	0	1	1	1
2. Calcitic layer	0	1	1	1	1
3. Number of aragonitic layers	0	1	2	2	0
4. Position of opercular nucleus	0	3	1	2	1
5. Opercular shape	0	1	0	1	1
6. Pigmentation pattern on head-foot region	0	0	1	1	1
7. Duct(s) for accessory boring organ and ventral pedal gland	0	0	0	1	1
8. Bursa copulatrix	0	2	1	1	0
9. Seminal receptacles at dorsal periphery of albumen gland	0	1	0	0	0
10. Penial shape	0	2	1	0	0
11. Penial vas deferens	0	1	0	0	2
12. Prostate	0	1	0	0	0
13. Accessory salivary gland(s)	0	1	1	2	2
14. Straw-like membrane around gland of Leiblein	0	0	1	1	1
15. Posterior duct of gland of Leiblein	0	0	1	1	1
16. Central cusp of rachidian	0	0	0	1	1
17. Margin of rachidian basal plate	0	0	1	1	1

Isla de los Estados, Tierra del Fuego, Argentina (LACM 71-289); Punta Catalina, Isla Grande, Tierra del Fuego, Chile (LACM 80-87.2) (4 ♀, 3 ♂).

Ocenebra erinacea; Roscoff, France (MCZ 298425) (2 ♀, 1 ♂).

Morphological data were compiled from soft tissues, radulae, shell ultrastructures, protoconchs, and opercula. Living specimens of *Nucella* and preserved specimens of *Nucella*, *Trophon* and *Ocenebra* were dissected.

Radulae (2-4 per species) were cleaned using a potassium hydroxide solution, rinsed in distilled water, air-dried, sputter-coated with carbon and gold, and examined with a Hitachi S-570 scanning electron microscope. Photomicrographs were taken of the unused, matured central portion of each radular ribbon.

Shell fragments from at least two individuals of each species were obtained by crushing the shell. Portions from the central region of the body whorl about one-half to three-quarters of a whorl away from the edge of the apertural lip were mounted, sputter-coated with carbon and gold, and their fracture surfaces observed with a Hitachi S-570 scanning electron microscope. An apparently amorphous outer layer was interpreted as consisting of calcite, while layers with organization in crystal lamellar structure were considered aragonitic (data from x-ray diffraction methods confirm these identifications; Kool and Harasewych, in preparation).

Cladistic Analysis: Seventeen characters, divided into 41 character states (Table 1), were used in a cladistic analysis performed with Hennig86 (Copyright J.S. Farris, 1988). The six multistate characters were entered as unordered. Most characters were derived from soft tissues (mainly from the male and female reproductive and alimentary systems), the remainder from radulae, opercula, protoconchs, and shell ultrastructure. Two additional species, *Thais nodosa* and *Muricanthus fulvescens* (Sowerby, 1841), are used in the cladistic analysis, based on data in Kool (1989; 1993, in press). *Muricanthus fulvescens*, a muricine and member of a sister group of Ocenebrinae, Trophoninae and Rapaninae, is used as outgroup for the cladistic analysis.

Table 1 lists characters and character states, and reflects the sequence in which organs and other morphological features are described for each of the three species.

RESULTS

DESCRIPTIONS OF TAXA

Nucella lapillus:

Shell: Protoconch (Figs. 26, 29) conical, low, of about 1¼ smooth whorls, with impressed suture; transition to teleoconch smooth, difficult to discern. Teleoconch highly polymorphic; usually elongate, oval, of 6-7 whorls (Figs. 1-6, 21, 22). Adult shell to 55 mm in height, 30 mm in width. Body whorl rounded, about 80% of shell height, smooth or sculptured with pattern of about 15 spiral, occasionally lamellose, ridges. Aperture (to 65% of shell height) oval; outer lip wide, smooth, occasionally with 3-4 denticles on edge of thickened lip. Columella with moderate callus, flat to concave. Siphonal canal short, open (Fig. 3) to partly closed (Fig. 1). Siphonal fasciole poorly developed, adjacent to callus layer. Shell color variable: white, grey, yellow, brown, orange-red; often banded; aperture, columella white.

Shell Ultrastructure: Innermost layer of crossed-lamellar

aragonite, with crystal planes oriented perpendicular to growing edge [15-20% of thickness; often absent (Fig. 28)]; middle layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [15-25% of thickness]; outermost layer of calcite [55-85% of thickness] (Fig. 27).

Operculum: D-shaped, with lateral nucleus just below center right (Figs. 7, 8). Outer surface (Fig. 7) with arch-shaped growth lines recurved at both ends; inner surface (Fig. 8) with 3-5 arch-shaped growth lines, with broad (35-40% of opercular width), callused, glazed outer rim.

Head and Foot: Uniformly light yellow to white. Cephalic tentacles elongate, thin. Incurrent siphon short. Mantle edge smooth. Accessory boring organ (Fig. 56, abo) large, well developed, (in females) anterior to, separate from equally large ventral pedal gland (Fig. 56, pg).

Mantle Cavity: Osphradium slightly more than ⅓ ctenidial length, less than ½ ctenidial width. Right pectin usually wider than left. Each lamella (8-10/mm) attached to mantle roof along ½ its base. Anteriormost portion of ctenidium straight, extending slightly anterior of osphradium. Ctenidial lamellae (9-11/mm) wider than high or equally wide as high, with strongly convex or straight lateral edges, translucent. Thick supporting rod extending beyond lateral edge of each lamella, forming small papilla.

Female Reproductive System: Vaginal opening round with slightly swollen edges, located below and posterior to anus. Bursa copulatrix (Fig. 47, 48, bc) small diverticulum, connected to vagina, ventral channel (vc) by wide ventral passage. Ventral channel formed by two small interlocking flanges located under ventral lobe of capsule gland, one arising from left lobe, the other from ventral epithelium. Single-chambered ingesting gland located between capsule gland and albumen gland. Albumen gland (Fig. 49) arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd), posteriorly into oviduct (od). Ovary yellow to light golden. Many specimens with pseudo-penis of variable size (see also Bryan *et al.*, 1986).

Male Reproductive System: Penis (Fig. 60) simple, elongate, dorso-ventrally flattened, often slightly curved, with abruptly tapering, papilla-like end. Penial vas deferens (Fig. 62, pvd) minute, simple duct, semi-closed by transverse ridges on overlapping ventral and dorsal sides of penis. Cephalic vas deferens (Fig. 57, cvd) well developed, extending from penis (p) to prostate gland (pr). Prostate gland (Fig. 57, pr) white; prostate duct (prd) dorso-ventral slit in cross section; duct open to mantle cavity posteriorly. Posterior vas deferens (along visceral mass) well developed, white to dirty white, iridescent. Testis light brown to golden.

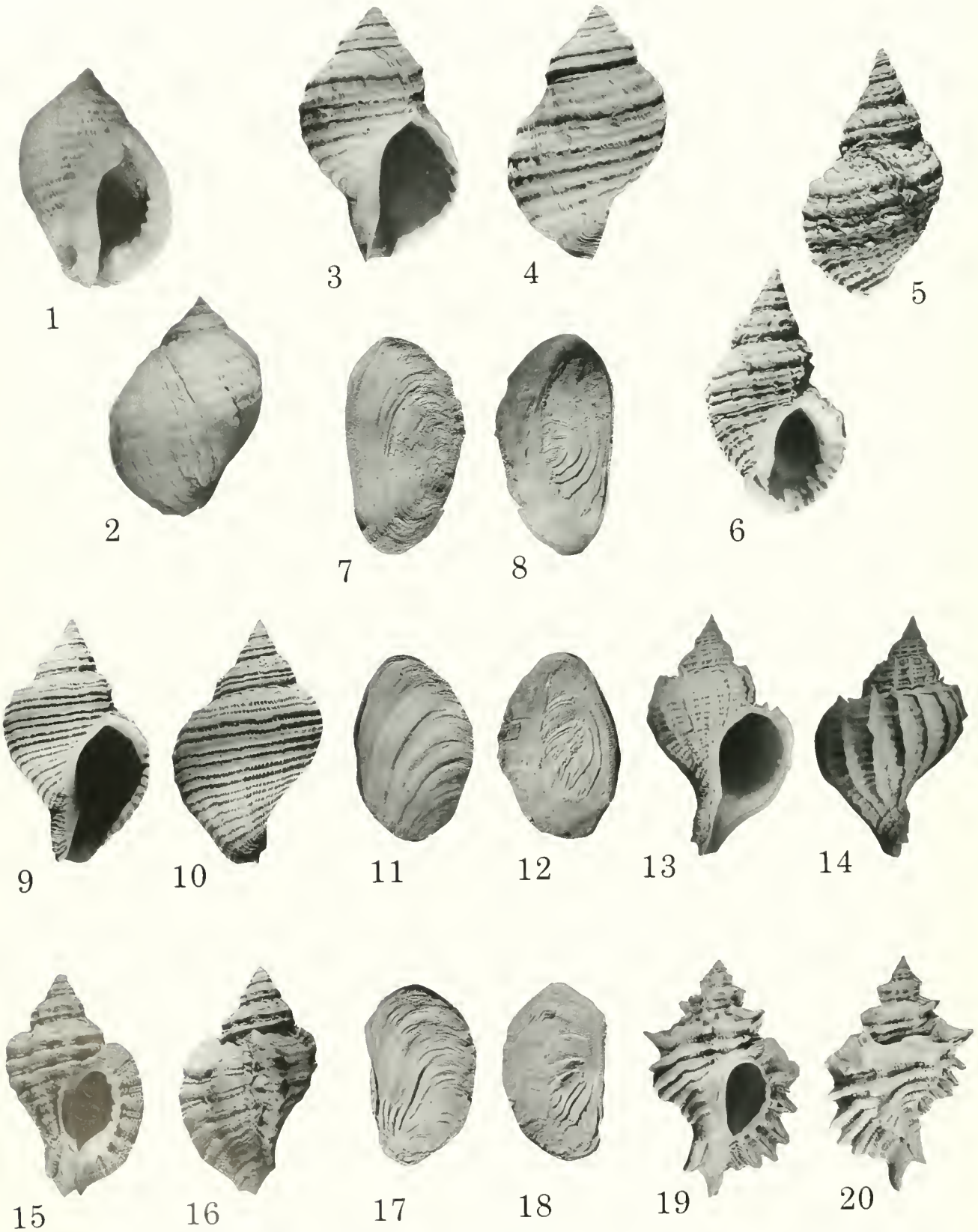
Alimentary System: Paired accessory salivary glands extremely long, usually equal to or slightly longer than one-half of shell height; left gland intertwined with salivary glands, right gland separate from salivary glands, situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior esophagus at some distance from valve. Glandular folds in mid-esophageal region inconspicuous. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct very short (<½ length of gland), with small terminal ampulla. Stomach tubular, with 8-12 large, radially oriented folds on wall. Stomach typhlosole extending dorsally onto left portion of posterior mixing area. Intestinal typhlosole thick, wide. Two digestive diverticula present. Rectal gland inconspicuous. Large papilla overlying equally large anus.

Radula: Ribbon length 30-35% of shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp of rachidian thin, flame-shaped, leaning more anteriorly (*in situ*) than lateral cusps; inner lateral denticle low on base of lateral cusp, occasionally bifurcate (within same specimen); outer edge of lateral cusp with several denticles; large marginal cusp pointing straight forward and parallel to elongate, lateral extension at base of rachidian tooth (Figs. 23-25), resulting in bifid appearance of rachidian basal plate. Lateral teeth shorter than rachidian width (Fig. 23).

Egg capsules: Elongate-oval, vase-shaped, up to 9 mm in height, 3 mm in width. Capsules yellow, light brown or purple (Lebour, 1937), each attached by short, thin stalk about 1 mm long. Apex tapered with rounded, cap-shaped top with mucous plug. Capsules interconnected at base. Number of embryos varying from two (Risbec, 1937) to one thousand (Fretter & Graham, 1962, 1985), most being nurse eggs (75-95%) (Crothers, 1985; Fretter & Graham, 1985; Lamy, 1928) (see also Pelseneer, 1911; Ankel, 1937; Thorson, 1941, 1946; Robertson, 1974).

Ecology: More is known about *Nucella* ecology than about any other muricoidean [for an extensive bibliography on the biology (primarily ecology) of *Nucella lapillus*, see Crothers, 1985]. *Nucella lapillus* and its western American congeners have been the topic of many comprehensive studies (Crothers, 1985; Emlen, 1966; Etter, 1987; Kincaid, 1957; Spight, 1972). *Nucella* feeds on barnacles and mussels (Colton, 1922; Connell, 1970; Crothers, 1973; Graham, 1955; Kool, 1987; Largen, 1967; Murdoch, 1969; Spight, 1982) in the rocky intertidal zone and is eaten by crabs and birds (Spight, 1976). Studies of Agersborg (1929), Colton (1922), and Moore (1936) show that environmental factors (wave action, food availability, etc.) influence shell morphology. Moore (1938) reported the main spawning period to be during winter and spring; but breeding occurs throughout the year (Lebour, 1937; Thorson, 1946). Juveniles hatch from the eggs after 4-7 months (Fretter & Graham, 1985).

Distribution: North Atlantic Ocean from southern Por-



Figures 1–8 *Nucella lapillus*. 1-6. Shells (**1,2** MCZ 69192, Freshwater Bay, Isle of Wright, England, height 25 mm; **3,4** MCZ 115093, Sullivan, Maine, U.S.A., height 35 mm, **5,6** MCZ 50600, Wales, height 34 mm). **7,8** Operculum (MCZ 302404, Braunton, North Devon, England, height 15 mm); **7** Outer surface; **8** Inner surface. **Figures 9-14** *Trophon geversianus*. Shells (**9,10** MCZ

tugal to Novaya Zemblya [records from western Mediterranean, Azores, Morocco, Senegal, and Canary Islands are suspect (Cooke, 1915)]; Great Britain; Ireland; Iceland; Greenland; New Jersey, U.S.A., to northern Canada [for extensive list of geographical range and localities, see Cooke, 1915].

Trophon geversianus:

Harasewych (1984) described aspects of the anatomy of *Trophon geversianus* (Figs. 9, 10, 13, 14, 30, 31). Because my observations were congruent with the descriptions in Harasewych's paper, only the most essential and supplemental data are presented to avoid unnecessary duplication.

Shell ultrastructure: Innermost layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [10-15% of thickness; often absent (Fig. 37)]; middle layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [15-20% of thickness]; outermost layer of calcite [70-80% of thickness] (Fig. 36).

Operculum: Ovate, with lateral nucleus in lower right (Figs. 11, 12). Outer surface (Fig. 11) with growth lines recurved at upper ends, progressively upright; inner surface (Fig. 12) with 3-4 narrow horseshoe-shaped growth lines, broad (>⅓ opercular width), lightly callused, glazed outer rim.

Head and foot: Uniformly light yellow. Cephalic tentacles elongate, thin. Incurrent siphon short. Mantle edge smooth. Accessory boring organ (Fig. 55, abo) well developed, sharing common duct with ventral pedal gland (pg) in females.

Mantle Cavity: Osphradium small (⅓-⅔ ctenidial length, ⅔ ctenidial width), usually partially overlying ctenidium. Right pectin usually wider than left. Each lamella (9-10 mm) attached to mantle roof along most of its length. Anteriormost portion of ctenidium straight, extending slightly anterior of osphradium. Ctenidial lamellae (10-12 mm) translucent, wider than high anteriorly, equally wide as high posteriorly, with straight to convex lateral edges.

Female Reproductive System: Vaginal opening (Fig. 47, vo) round, with swollen edges, located below, slightly anterior to anus. Bursa copulatrix (Figs. 47, 48, bc) small diverticulum, connected to vagina and ventral channel (vc) by wide duct. Wall of posterior vagina with folds decreasing in number posteriorly. Capsule gland with simple, inconspicuous ventral channel posteriorly connected to large, well-developed ingesting gland filled with whitish substance. Albumen gland (Fig. 49) large, arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd), posteriorly into oviduct (od).

Male Reproductive System: Penis (Fig. 59) bulbous, short, dorso-ventrally flattened, with large papilla. Penial vas deferens (Fig. 62, pvd) minute, simple duct, closed by overlapping ventral and dorsal sides of penis. Cephalic vas deferens (Fig. 57, cvd) well developed. Prostate gland (Fig. 57, pr) light yellow; prostate duct (prd) dorso-ventral slit in cross section; duct open to mantle cavity posteriorly.

Alimentary System: Paired accessory salivary glands short (<1 10 shell height); left gland intertwined with left salivary gland, right gland free, situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and elongate valve of Leiblein. Salivary ducts attached to anterior esophagus immediately anterior to valve. Glandular folds in mid-esophageal region well developed. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct short, without terminal ampulla. Stomach tubular, with 10-15 thin, elevated folds on wall; posterior ones oriented toward center, anterior ones merging into elevated section of sorting area. Intestinal typhlosole thin. Two digestive diverticula present. Rectal gland light brown, extending along ½ of pallial gonoduct.

Radula: Ribbon length 40-45% of shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp thin, with wide base; inner lateral denticle small protrusion from base of lateral cusps; outer edge of lateral cusp straight, with several faint denticles; large marginal cusp pointing straight forward and parallel to faint, elongate, lateral extension at base of rachidian tooth (Figs. 32-34), resulting in bifid appearance of rachidian basal plate. Lateral teeth shorter than rachidian width, with wide bases positioned close together (Fig. 32).

Egg capsules: Discoidal, laterally flattened, with wide, equally flattened base, up to 20 mm in height (including base), 12 mm in width (Harasewych, 1984, Fig. 23). Capsules yellowish in color, and containing 74-112 embryos (Melvill & Standen, 1898). Capsules deposited in rows with flattened edges adjacent to one another (Lamy, 1928; D'Asaro, 1991).

Ecology: This species lives in the rocky intertidal and subtidal zones where barnacles and mussels are plentiful.

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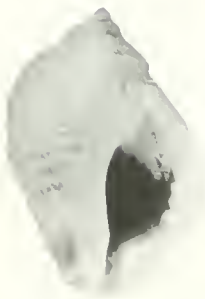
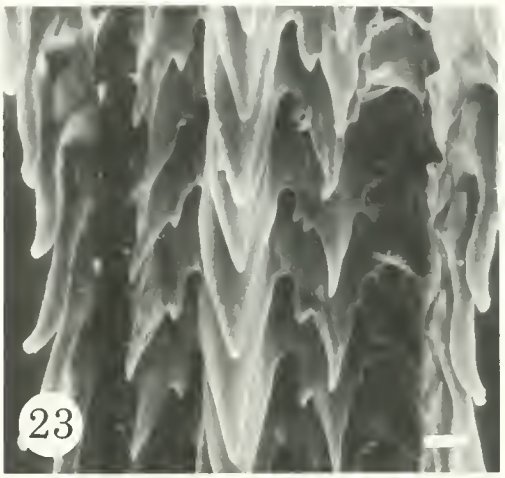
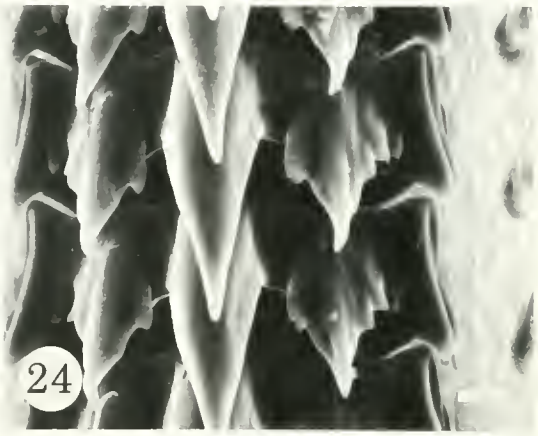
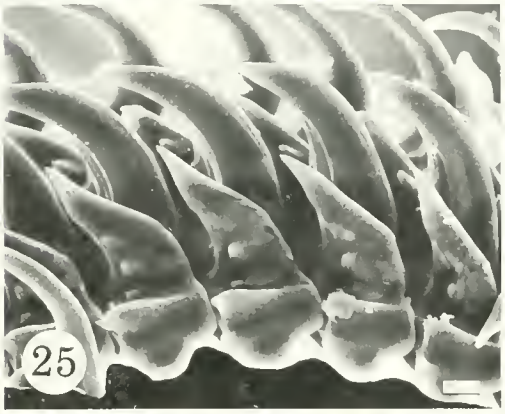
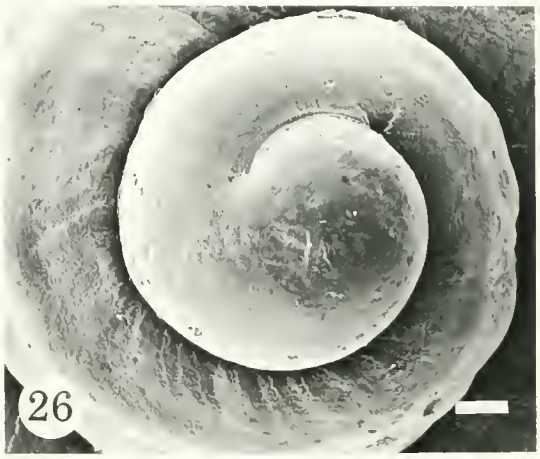
109413, Ushaia, Tierra del Fuego, Argentina, height 41 mm; **13,14** MCZ 132566, Falkland Islands, Argentina, height 47 mm). **11,12** Operculum (LACM 86-270 2, Daniel Este, Isla Grande, Tierra del Fuego, Chile, height 11 mm); **11** Outer surface; **12** Inner surface. **Figures 15-20** *Oocnebra crinacea* Shells (**15,16** MCZ 87662, Weymouth, England, height 31 mm; **19,20** MCZ 172450, Fos-sur-Mer, Bouches-du-Rhône, France, height 56 mm) Operculum (**17,18** MCZ 302405, St. Lunaire, France, height 8.0 mm); **17** Outer surface; **18** Inner surface.

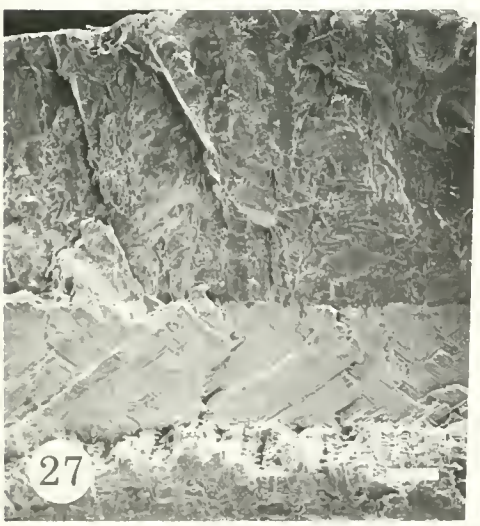


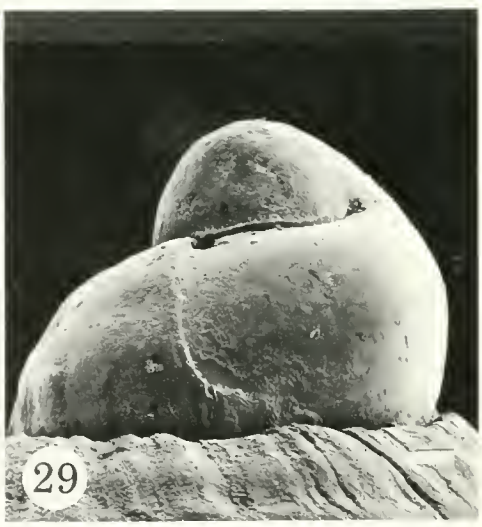




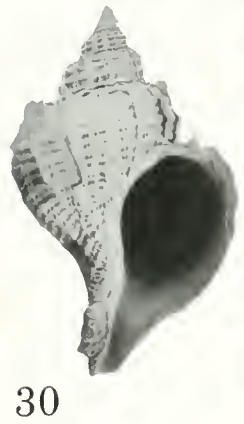


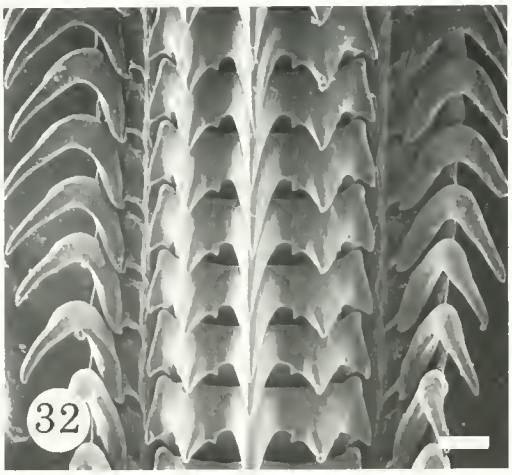


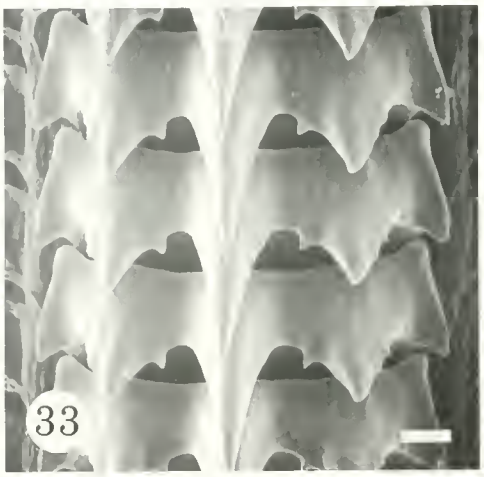


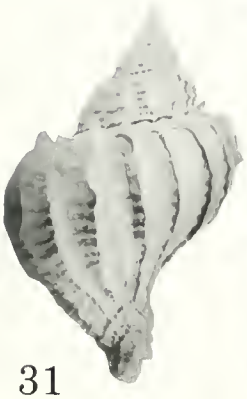


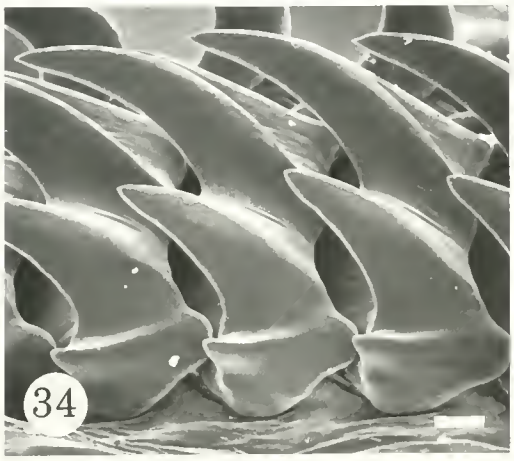
Figures 21–29 *Nucella lapillus*. **21,22** Shell (MCZ 69192, Freshwater Bay, Isle of Wight, England, height 25.1 mm). **23-25** Radula (USNM 857053, Kittery, Maine, U.S.A.). **23** Central portion of radular ribbon. Scale bar = 15 μm. **24**. Rachidian teeth. Scale bar = 10 μm. **25** Side view of rachidian teeth (right row of lateral teeth removed). Scale bar = 10 μm. **26,29**. Protoconch (MCZ 14184, Isle au Haut, Maine, U.S.A.). **26** Apical view. Scale bar = 12 μm. **29** Side view. Scale bar = 12 μm. **27,28**. Shell ultrastructure (view of growing edge; innermost layer on bottom) (MCZ 69192, Freshwater Bay, Isle of Wight, England). Scale bars, 45 μm and 70 μm, respectively.

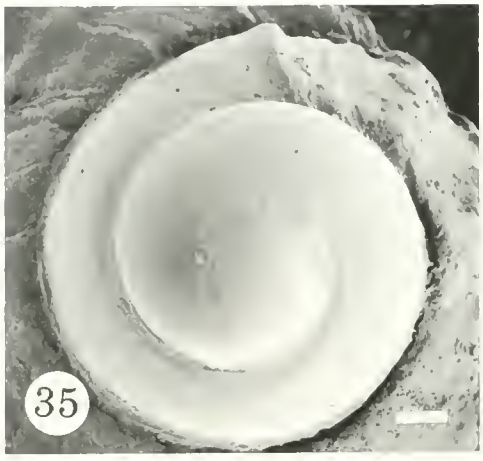




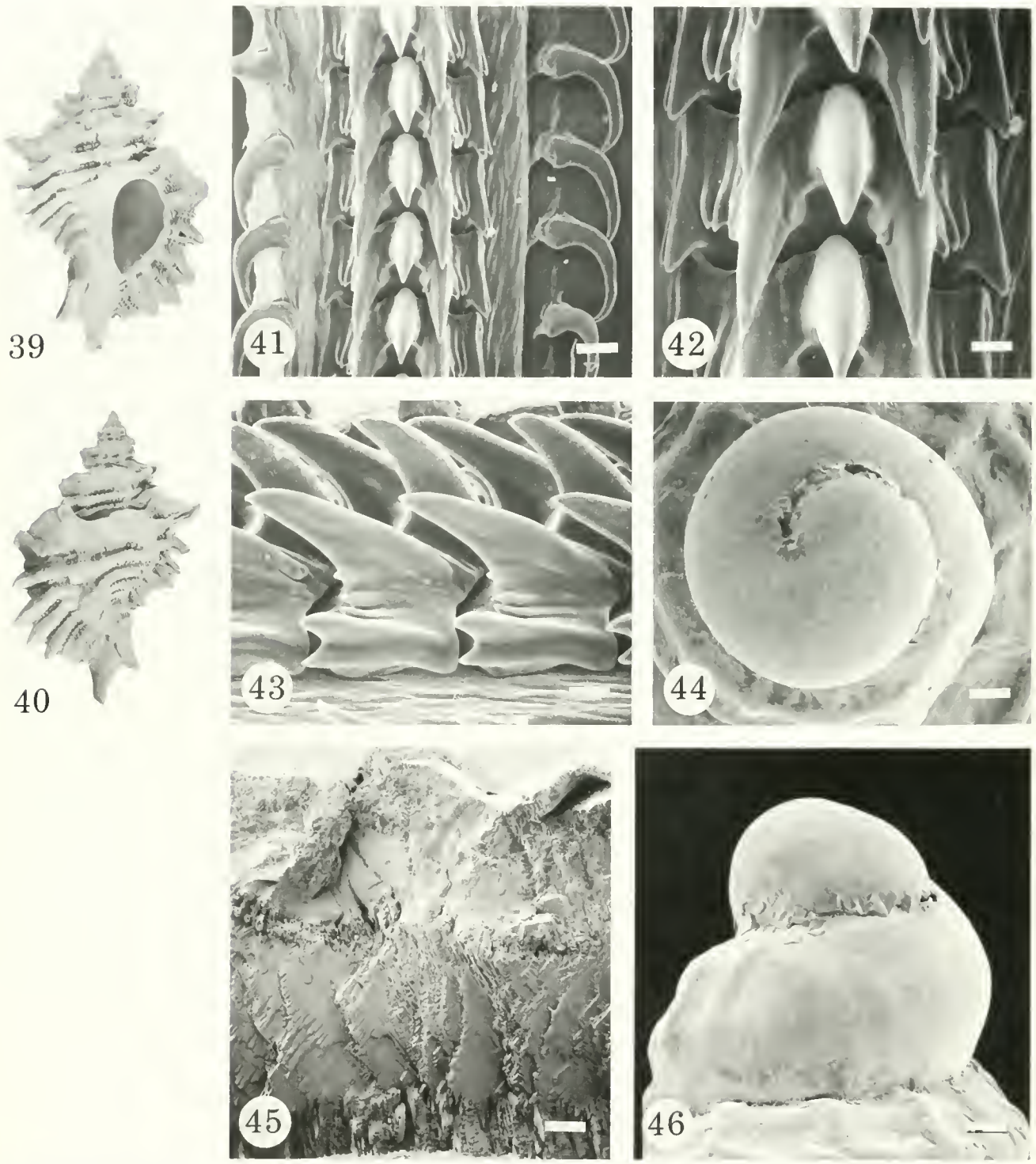




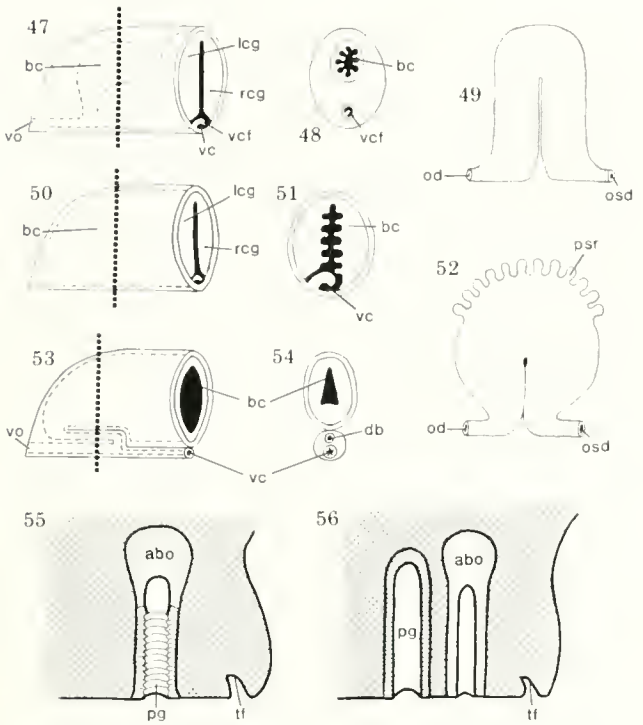




Figures 30–38 *Trophon geversianus*. **30.31** Shell (MCZ 132566, Falkland Islands, Argentina, height 47 mm). **32-34** Radula. (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile). **32** Central portion of radular ribbon. Scale bar = 45 μm. **33** Rachidian teeth. Scale bar = 25 μm. **34** Side view of rachidian teeth. Scale bar = 20 μm. **35.38** Protoconch (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile). **35** Apical view. Scale bar = 150 μm. **38** Side view. Scale bar = 150 μm. **36.37** Shell ultrastructure (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile); Scale bars, 60 μm and 150 μm, respectively.

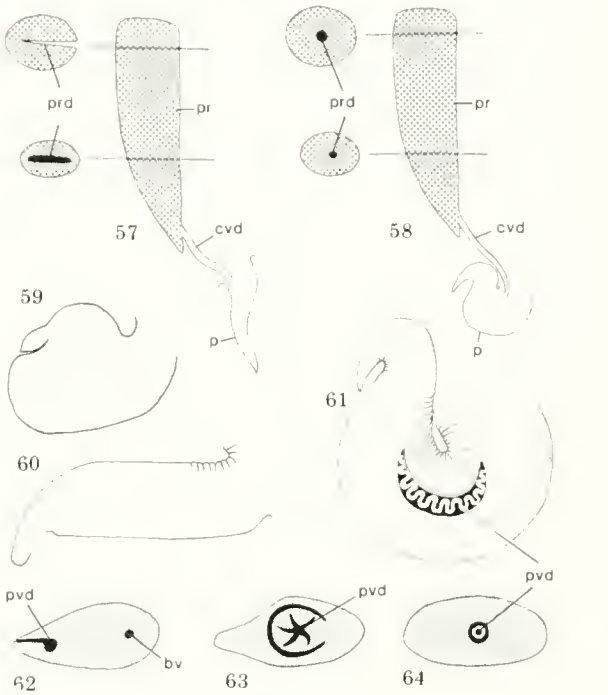


Figures 39–46 *Oceneblra erinacea*. **39,40** Shell (MCZ 172450, Fos-sur Mer, Bouches-du-Rhône, France, height 56 mm). **41–43** Radula (MCZ 298425, Roscoff, France). **41** Central portion of ribbon. Scale bar = 17 μm. **42** Rachidian teeth. Scale bar = 8 μm. **43** Side view of rachidian teeth. Scale bar = 9 μm. **44,46** Protoconch (MCZ 38369, Kent, England). **44** Apical view. Scale bar = 90 μm. **46** Side view. Scale bar = 90 μm. **45** Shell ultrastructure (MCZ 298425, Roscoff, France). Scale bar = 130 μm.



Figures 47–56 Anatomical structures of the female reproductive system of *Nucella lapillus*, *Trophon geversianus*, *Ocenebra erinacea*, *Muricanthus fulvescens*, and *Thais nodosa* **47,50,53** Bursa copulatrix in *N. lapillus* and *T. geversianus* (**47**), *Th. nodosa* (**50**), *O. erinacea* and *M. fulvescens* (**53**). **48,51,54** Cross sections through bursa copulatrix (location indicated by vertical bar). **49,52** Albumen glands in *N. lapillus*, *T. geversianus*, *O. erinacea*, *M. fulvescens* (**49**), and *Th. nodosa* (**52**). **55,56** Sagittal section through foot showing accessory boring organ and pedal gland of *Th. nodosa*, *T. geversianus*, *M. fulvescens* (**55**), *N. lapillus*, and *O. erinacea* (**56**).

abo, accessory boring organ; bc, bursa copulatrix; db, duct to bursa copulatrix; lcg, left lobe of capsule gland; od, oviduct; osd, ovi-sperm duct; pg, ventral pedal gland; psr, posterior seminal receptacles; rcg, right lobe of capsule gland; tf, transverse fold; vc, ventral channel; vcf, flange of the ventral channel; vo, vaginal opening



Figures 57–64 Anatomical structures of the male reproductive system of *Nucella lapillus*, *Trophon geversianus*, *Ocenebra erinacea*, *Muricanthus fulvescens*, and *Thais nodosa*. Prostate gland with proximal and distal cross sections in *N. lapillus*, *T. geversianus*, *O. erinacea*, *M. fulvescens* (**57**) and *Th. nodosa* (**58**). Penial morphologies with cross sections in *T. geversianus* (**59,62**), *N. lapillus*, *M. fulvescens* (**60,62**), *O. erinacea* (**60,63**), and *Th. nodosa* (**61,64**).

bv, blood vessel; cvd, cephalic vas deferens; p, penis; pr, prostate; prd, duct through prostate; pvd, penial vas deferens

Sculpture of the shell may vary with the type of habitat.

Distribution: Southern Argentina to Chile.

Ocenebra erinacea:

Shell: Protoconch (Figs. 44, 46) conical, low, of 1½ smooth whorls, and with impressed suture; transition to teleoconch smooth, difficult to discern. Teleoconch elongate, fusiform, biconical (Figs. 15, 16, 19, 20, 39, 40), of 7-8 whorls. Adult shell highly variable in shape, to 55 mm in height, 25 mm in width (not including spine length; 35 mm including spine length). Body whorl 55-60% of shell height, with 3-9 varices, often with frilled edges, and with 6-8 spiral cords. Aperture (to 30% of shell height) round to oval; outer lip with crenulated edge. Moderately callused columella. Siphonal canal partly or completely closed, often nearly equal in length to aperture in larger specimens. Siphonal fasciole pointing away from siphonal canal. Shell color yellowish to cream or dark brown; aperture, columella white.

Shell ultrastructure: Innermost layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [15-20% of thickness]; followed by layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [40-45% of thickness]; followed by layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [5-8% of thickness]; outermost layer of calcite [35% of thickness] (Fig. 45).

Operculum: D-shaped, with lateral nucleus in lower right (Figs. 17, 18). Outer surface (Fig. 17) with arch-shaped growth lines progressively upright, recurved at upper end; inner surface (Fig. 18) with 4-5 arch-shaped growth lines, with broad (≈ ½ opercular width), lightly callused, glazed outer rim.

Head and foot: Uniformly light yellow to white. Cephalic tentacles elongate, thin. Incurrent siphon well developed. Mantle edge smooth, occasionally with crenulations (possibly an artifact). Sole of foot with large lateral

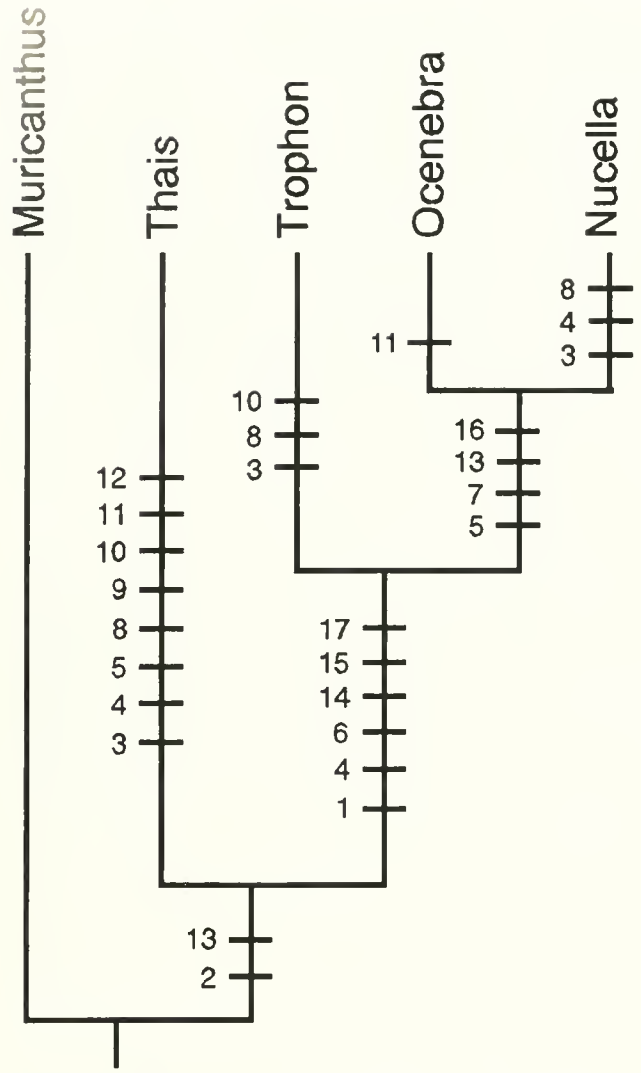


Figure 65 Cladogram, based on analysis of data in Table 1, showing high phylogenetic affinity between *Nucella* and *Ocenebra*. Numbers next to character changes correspond to numbers given to characters in Table 1. Alternative, equally parsimonious character state transformation series are possible for characters 3, 4, 5, and 8 (see text).

folds. Accessory boring organ (Fig. 56, abo) large, well developed, (in females) anterior to, separate from equally large ventral pedal gland (Fig. 56, pg).

Mantle Cavity: Osphradium (<½ ctenidial length, ¾ ctenidial width) partially extending over ctenidium. Right pectin usually wider than left. Each lamella (10-11/mm) attached to mantle roof along short basal portion. Anteriormost portion of ctenidium straight, extending anteriorly of osphradium. Ctenidial lamellae (11-12/mm) basically triangular, longer than high with convex lateral edges posteriorly. Lamellar support rods not well developed.

Female Reproductive System: Vaginal opening (Fig. 53, vo) round to elongate, on short, extension of pallial gonoduct, situated below, posterior to anus. Bursa copulatrix (Figs. 53, 54, bc) large diverticulum (equal in diameter to capsule gland), connected at its anterior portion to duct running parallel to ventral channel for some length prior to connecting with it (Figs. 53, 54, db). Lumen of bursa copulatrix filled with loose flocculent material and iridescent spherules. Capsule gland posterior to, shorter than bursa copulatrix. Ventral channel (Figures 53, 54, vc) well developed anteriorly, less distinct posteriorly. Ingesting gland situated between capsule gland, albumen gland. Albumen gland (Fig. 49) arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd) posteriorly into oviduct (od). Ovary orange-yellow. Pseudo-penis occasionally present (see also Féral, 1976).

Male Reproductive System: Penis (Fig. 60) simple, dorso-ventrally flattened, elongate, slightly curved, with abruptly tapering, papilla-like end. Penial vas deferens (Fig. 63, pvd) a wide, straight tube star-shaped in cross section; tube partially attached to penial wall. Cephalic vas deferens (Fig. 57, cvd) large, similar to penial vas deferens in structure, extending from penis (p) to prostate gland (pr). Prostate gland (Fig. 57, pr) white to yellow; prostate duct (prd) a dorso-ventral slit in cross section anteriorly, a triangular large space posteriorly; duct open to mantle cavity posteriorly (Fig. 57). Posterior vas deferens white to dirty white, iridescent. Testis yellowish.

Alimentary System: Paired accessory salivary glands very long (≈ ½ shell height); left gland intertwined with left salivary gland, right gland free,situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior esophagus at short distance from valve. Glandular folds in mid-esophageal region swollen, especially well developed at connecting point between esophagus and gland of Leiblein. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct very short (<½ length gland of Leiblein), with prominent terminal ampulla. Stomach tubular, with faint folds on stomach wall oriented toward center of stomach (poorly preserved in specimens examined). Rectal gland thin, green, extending along ½ of pallial gonoduct. Large papilla overlaying anus.

Radula: Ribbon length 35-40% shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp of rachidian thin, flame-shaped, leaning more anteriorly (*in situ*) than lateral cusps; inner lateral denticle low on base of lateral cusp, occasionally bifurcate (within same specimen); outer edge of lateral cusp straight, with several short denticles; large marginal cusp pointing straight forward and parallel to elongate, lateral extension at base of rachidian tooth (Figs. 41-43), resulting in bifid appearance of rachidian basal plate. Lateral teeth with narrow base, widely spaced, shorter than rachidian width (Fig. 41).

Egg capsules: Oval-elongate, vase-shaped, triangular in cross section. Capsules yellowish, up to 13 mm in height, 6 mm in width, each on narrow stalk, attached by flat base. Apex with short elevated protuberance with mucous plug. Each capsule containing 4-167 embryos, of which none are nurse eggs (Fretter & Graham, 1985; Lebour, 1937).

Ecology: *Ocenebra erinacea* lives in the rocky intertidal and subtidal zones (Jeffreys, 1867) to 150 meters (Fretter & Graham, 1985) where it feeds on oysters and other bivalves (Fretter & Graham, 1985), barnacles and limpets (Graham, 1955). Lebour (1937) reported breeding in late spring and summer. Juveniles hatch from the eggs after 12-14 weeks (Fretter & Graham, 1985). A comprehensive ecophysiological study was done on *Ocenebra erinacea* by Hawkins (1985).

Distribution: North Atlantic Ocean (Spain to Norway, Great Britain, Ireland); Mediterranean Sea (southern Europe, northern Africa).

CLADISTIC ANALYSIS

The cladistic analysis yielded one tree with a consistency index of 0.88 (Fig. 65). This cladogram indicates that 1) placement of *Nucella* in Thaidinae or its senior synonym, Rapaninae, creates polyphyletic groups (see also Kool, 1989); 2) *Nucella* is more closely related to *Ocenebra* than to *Trophon* and should be placed in Ocenebrinae; 3) the subfamilial boundaries between Ocenebrinae and Trophoninae are much less distinct than previously accepted.

Characters and character state distribution among the taxa Nucella, Trophon, Ocenebra, Thais, and the outgroup, Muricanthus:

Character 1. Protoconch: 0. multispiral (> 2 whorls); 1. paucispiral (≤ 1½ whorls).

Nucella, *Trophon* and *Ocenebra* (Figs. 26, 29, 35, 38, 44, 46) have a paucispiral, smooth protoconch without a sinusigeral notch or outwardly-flared lip. This morphology reflects direct development. The outgroup and the rapanines have a multispiral (and generally sculptured) protoconch with a sinusigeral notch and outward-flaring lip, typical for species with a planktonic larval stage.

Character 2. Calcitic layer: 0. absent; 1. present.

The outgroup lacks an outer calcitic shell layer that is present in the other four taxa. The presence of calcite appears to be the derived condition.

Character 3. Number of aragonitic layers: 0. 3; 1. 4; 2. 2.

The outgroup and *Ocenebra* have three layers of aragonite (transverse, collabral, transverse). *Thais* has an additional, innermost fourth layer of crystals oriented in a 45° angle; both *Nucella* and *Trophon* have two layers (transverse, collabral), but may lack the innermost transverse layer (Figs. 28, 37).

Character 4. Nucleus of operculum: 0. terminal nucleus in lower right; 1. lateral nucleus in lower right; 2. lateral nucleus below center right; 3. lateral nucleus in center right.

The outgroup has a terminal nucleus in the lower right. All ingroup taxa have a lateral nucleus, the position of which varies. The nucleus of the operculum in *Nucella* is located below the center right; that of *Trophon* and *Ocenebra* in the lower right (Figs. 7, 11, 17, respectively). The nucleus is located in the center right in rapanines.

Character 5. Shape of operculum: 0. oval; 1. D-shaped.

The opercula of *Nucella*, *Thais*, and *Ocenebra* are roughly D-shaped. Those of *Muricanthus* and *Trophon* are elongate-oval.

Character 6. Pigmentation pattern of head-foot region: 0. present; flecked with black and gray; 1. absent, uniformly colored (faint yellow).

The head-foot regions of *Nucella*, *Trophon*, and *Ocenebra* are uniformly faint yellow. Both *Thais* and the outgroup are densely flecked with black blotches and specks (this pattern generally survives preservation in alcohol although other colors, such as white and yellow, fade).

Character 7. Ventral pedal gland and accessory boring organ: 0. sharing one duct; 1. with separate ducts.

In *Nucella* and *Ocenebra*, the accessory boring organ and ventral pedal gland (Fig. 56, abo, pg) have separate ducts to the sole of the foot, while in *Trophon*, rapanines, and the outgroup these structures share a common duct (Fig. 55, abo, pg).

Character 8. Bursa copulatrix: 0. large diverticulum, separate from capsule gland; 1. small diverticulum, separate from capsule gland; 2. small chamber with lumen continuous with capsule gland.

The bursa copulatrix is a small blind sack in *Nucella* and *Trophon* (Fig. 47), a large separate diverticulum in *Ocenebra* (Fig. 53) and the outgroup, while in rapanines the bursa is continuous with the capsule gland (Figs. 50, 51).

Character 9. Seminal receptacles at dorsal periphery of albumen gland: 0. absent; 1. present.

In *Thais*, a row of posterior seminal receptacles (Fig. 52, psr) at the dorsal periphery of the albumen gland presumably increases efficiency in the fertilization process (Kool, 1988, 1989). These posterior seminal receptacles are absent in *Nucella*, *Trophon*, *Ocenebra*, and in the outgroup, *Muricanthus* (Fig. 49). This character is a synapomorphy for Rapaninae (Kool, 1993, in press).

Character 10. Penial shape: 0. simple, elongate to lightly curved; 1. bulbous, with papilla; 2. strongly recurved with pseudo-papilla.

Penial shape in *Nucella*, *Ocenebra*, and the outgroup is elongate (Fig. 60). The penis in *Thais* is strongly recurved, and sinuous (Fig. 61), while that of *Trophon* is short, bulbous, with a distinct papilla (Fig. 59).

Character 11. Penial vas deferens: 0. simple duct; 1. small, loose duct-within-a-duct; 2. large duct-within-a-duct, partially attached to penial inner wall.

Nucella, *Trophon* and the outgroup have a penial vas deferens that is loosely closed, while rapanines have a "duct-within-a-duct" system (Figs. 61, 64) (Kool, 1988, 1989). *Ocenebra* differs from both types in having a rather wide inner duct that is partially attached to the penial inner wall (Fig. 63).

Character 12. Prostate Gland: 0. open to mantle cavity posteriorly; 1. without opening to mantle cavity.

Males of *Nucella*, *Trophon*, *Ocenebra*, and the outgroup have a prostate gland that is open to the mantle cavity along its posterior portion (Fig. 57). The prostate of rapanine males does not open to the mantle cavity (Fig. 58).

Character 13. Accessory salivary gland length: 0. right gland small, left gland absent; 1. glands < ¼ shell height; 2. glands ≥ ½ shell height.

Character 14. Straw-like membrane around gland of Leiblein: 0. present; 1. absent.

In most rapanines and the outgroup, the gland of Leiblein is covered by a thick membrane of interwoven fibers of connective tissue, producing a straw-like appearance. Such a membrane is absent in *Nucella*, *Trophon* and *Ocenebra*.

Character 15. Posterior duct of gland of Leiblein: 0. longer than ½ of gland length; 1. shorter than ½ gland length.

In *Nucella*, *Trophon* and *Ocenebra*, the gland of Leiblein tapers posteriorly into a thin, very short posterior duct that runs adjacent to the posterior esophagus and is often filled with secretory material from the gland; in the majority of rapanines and in the outgroup this duct is much longer, extending into the dorsal branch of the afferent renal vein.

Character 16. Central cusp of rachidian: 0. oriented in same plane as lateral cusps; 1. leaning more anteriorly than lateral cusps.

In *Nucella* (Fig. 25) and *Ocenebra* (Fig. 43) the central cusp on the rachidian leans more anteriorly (*in situ*) than the lateral cusps. In *Thais*, *Trophon* (Fig. 34), and the outgroup, the lateral cusps and central cusp are aligned in the same plane.

Character 17. Margin of rachidian basal plate: 0. straight; 1. bifid.

The bifid condition of the rachidian basal plate (Figs. 25, 34, most developed in Fig. 43) is found in *Nucella*, *Trophon* and *Ocenebra*, but not in *Thais* or the outgroup.

Synapomorphies for the Nucella-Ocenebra clade (*Fig.* 65):

Character 5: The character for opercular shape is homoplastic; a D-shaped operculum occurs in *Thais* as well.

Character 7: Both *Nucella* and *Ocenebra* have separate openings for the ventral pedal gland and accessory boring organ (Fig. 56, abo, pg). Female specimens of *Trophon geversianus*, *Thais nodosa*, and the outgroup, have a single duct and opening for these organs (Fig. 55, abo, pg). A shared duct for the accessory boring organ and ventral pedal gland, as found in *Trophon geversianus*, may not be as advantageous as an arrangement as when the ducts originating from the accessory boring organ and ventral pedal gland are separate. It would appear that an arrangement where one duct serves both as ventral pedal gland and as a passage for the accessory boring organ and its secretions during boring activities (Carriker, 1981) prevents the female from boring activity, and thus perhaps feeding in general, during stages of egg-laying.

Character 13: *Nucella* and *Ocenebra* have a pair of very long accessory salivary glands (≥ ½ shell height). *Trophon* and *Thais* have much smaller glands (< ¼ shell height). The outgroup has only one extremely small right accessory salivary gland.

Character 16: In *Nucella*, and to a much greater degree in *Ocenebra*, the central cusp leans more anteriorly (Figs. 25, 43, respectively) (*in situ*) than the lateral cusps, whereas in *Trophon*, the central cusp is aligned with the lateral cusps (Fig. 34).

Synapomorphies for the Trophon-Nucella-Ocenebra Clade:

Character 1: The paucispiral protoconch is indicative of having crawl-away larvae, rather than a planktonic larval stage that is found in *Thais* and other rapanines (Kool, 1993, in press) and the outgroup.

Character 4: The cladogram suggests that an opercular nucleus below the center right (*Nucella*; character state 2) evolved from the ancestral condition for the taxa in this clade of having a nucleus in the lower right (*Ocenebra* and *Trophon*; character state 1).

Character 6: All three taxa lack a pigmentation pattern on their head-foot region that is found in the outgroup, *Thais*, and other members of the Rapaninae.

Character 14: The straw-like outer membrane of the gland of Leiblein is absent in the species of this clade, but present in the outgroup, and most members of Rapaninae (Kool, 1989; 1993, in press).

Character 15: The posterior duct of the gland of Leiblein is shorter than ½ the length of the gland itself in this clade, but much longer in the remaining taxa, reaching into the dorsal branch of the afferent renal vein.

Character 17: The bifid condition of the basal plate, especially well developed in *Ocenebra* (Fig. 43), is absent in *Thais* and the outgroup.

Synapomorphies for the Thais-Trophon-Nucella-Ocenebra Clade:

Character 2: An outer layer of calcite is present in all ingroup taxa, but is absent in the outgroup.

Character 13: The outgroup has only one extremely small right accessory salivary gland. A situation of having a pair of medium-size accessory salivary glands appears to

have evolved from the condition described above and to have given rise to the most derived condition (extremely long glands).

DISCUSSION

According to the topology of the cladogram (Fig. 65), two characters have evolved in a parallel manner in *Nucella lapillus* and *Trophon geversianus*. Out of the context of the cladogram, these similarities would suggest a closer relationship between these two species than is suggested by the tree topology:

Character 3: Shell ultrastructure in both *Nucella* and *Trophon* consists of two aragonitic layers and an outer layer of calcite. Specimens of both may lack the innermost (transverse) layer (Figs. 28, 37). More detailed studies may reveal the cause of this variation. Perhaps environmental factors may play a role (Etter, personal communication).

Character 8: The morphology of the bursa copulatrix of *Nucella* is very similar to that of *Trophon*. In both taxa, a relatively small, muscular blind sack branches off from the vagina (Figs. 47, 48). In *Ocenebra* the bursa is thin-walled and equal in width and height to the capsule gland, extending for up to ½ the length of the pallial complex. The ventral channel loops backwards towards the anterior portion of the bursa in *Ocenebra* (Fig. 53), rather than straight up into the bursa as in *Trophon* and *Nucella* (Fig. 47).

The above two characters could be considered synapomorphies for an alternative, but less parsimonious, tree in which *Trophon* and *Nucella* would be united in one clade. However, in the proposed phylogenetic hypothesis (Fig. 65), four synapomorphies support a clade consisting of *Nucella* and *Ocenebra*, rendering the above two characters as homoplastic.

Fretter and Graham (1962) mention several similarities in egg capsule morphology between *Nucella lapillus* and *Ocenebra erinacea*. Both species lay vase-shaped capsules, whereas *Trophon geversianus* produces discoidal egg capsules. However, having discoidal egg capsules is only an autapomorphic trait for *Trophon* and does not provide clues about relationship in this case. Alternative, equally parsimonious transformation series are possible for characters 3, 4, 5, and 8. For Characters 3, 5, and 8, I chose the scenario involving homoplasy over one involving a reversal to avoid an "artificial" increase in synapomorphies. Similarly, for Character 4, I chose the least linear trans-formation series ("zero state" evolving into both the "three state" and the "one state").

Zoogeographical data reveal that members of *Nucella*, *Ocenebra* and *Trophon* occur primarily in colder waters of the temperate and boreal zones, whereas rapanines and the outgroup occur primarily in warmer waters of the (sub)tropics (Kool, 1989).

Nucella lapillus and *Ocenebra erinacea* overlap for much of their ranges in primarily temperate western European waters. In addition, *N. lapillus* occurs in the western Atlantic, where *O. erinacea* does not, and *O. erinacea* occurs in the Mediterranean, where *N. lapillus* has not occurred since the Pleistocene [Malatesta (1960) cited records of *N. lapillus* from the Pleistocene of Sicily]. Cooke (1915), in a comprehensive list of localities for *Nucella lapillus*, showed that the southernmost record for this species is the Algarve coast of Portugal and alleged that any records from Northern Africa (see Nordsieck, 1982), the western Mediterranean, the Azores, and the Canary Islands, are highly suspect. Other members of what can be assumed to be *Ocenebra s.s.* and *Nucella s.s.* are found in the eastern Pacific (Abbott, 1974) and the northern Pacific. Furthermore, *Ocenebra s.s.* occurs in western Africa (Houart, 1989) and South Africa (Kilburn & Rippey, 1982). Ranges of these genera may be revised when more *Ocenebra*-like taxa (for example from Japan) and *Nucella*-like species have been examined with respect to their anatomy, radula, shell ultrastructure, etc. Such studies are also necessary to determine if, for example, species such as *Nucella dubia* and *Nucella squamosa*, both from the South African Province, are indeed members of *Nucella s.s.* It appears from preliminary dissections that the genus *Nucella* can no longer be considered restricted to the temperate waters of the northern hemisphere (Kool, in preparation).

Trophon geversianus, limited to the South American continent, lives in temperate to boreal waters, as do *Nucella lapillus* and *Ocenebra erinacea*.

SYSTEMATIC CONCLUSIONS

The high degree of similarity in anatomy, radula, protoconch, shell ultrastructure and opercular in *Ocenebra erinacea*, *Trophon geversianus* and *Nucella lapillus* indicates that these three taxa are more closely related to one another than any one of them is to *Thais* or other representatives of Rapaninae. *Nucella* should therefore be excluded from Rapaninae to maintain monophyly (Kool, 1989; 1993, in press). The difficulty of correctly allocating *Nucella* to a subfamily is indicative of the dilemma of our lack of understanding of higher muricoidean systematics. The cladistic analysis and the resulting cladogram (Fig. 65) suggest that *Nucella* is better placed in Ocenebrinae than in Trophoninae. It is obvious that the boundaries of groups at the higher taxonomic categories, traditionally based on shell characters, become less clear after completion of thorough anatomical studies of members from different genera and subfamilies. Results shown here suggest that *Trophon geversianus*, the type species of Trophoninae, is closely related to *Nucella* and *Ocenebra*. Perhaps it is more closely related to the latter two taxa than to other species hitherto included in Trophoninae. It is beyond the scope of this paper to suggest synonymization of Trophoninae with Ocenebrinae. However, I suspect that future studies will show that Trophoninae is not a monophyletic group and that a new name for some of its members may be warranted. The following systematic arrangement is proposed for the taxa treated herein:

MURICOIDEA Rafinesque, 1815
MURICIDAE Rafinesque, 1815
RAPANINAE Gray, 1853 (*sensu* Kool, 1993, in press)
Thais Röding, 1798
OCENEBRINAE Cossmann, 1903
Ocenebra Gray, 1847
Nucella Röding, 1798
TROPHONINAE Cossmann, 1903)
Trophon Montfort, 1810

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Thala esperanza, a new Costellariidae (Mollusca: Gastropoda) from northern Puerto Rico

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ABSTRACT

Thala esperanza n. sp. is described from Playa Esperanza, municipality of Manati, on the northern coast of Puerto Rico. Small size, slender and delicate shell, smaller spire angle, larger number of spiral cords, and a distinctive constriction below the suture separates the new taxon from western Atlantic congeneric species.

Key words: *Thala*, Costellariidae, Puerto Rico, Atlantic Ocean, Caribbean Sea, new species, systematics.

INTRODUCTION

The costellariid genus *Thala* H. & A. Adams, 1853 comprises about 12 Recent species, of which two are known from the western Atlantic. *Thala foveata* (Sowerby, 1834) is known to occur at St. Vincent, Antilles and possibly at the island of São Thomé in the eastern Atlantic (Maes & Raeihle, 1975). *Thala floridana* (Dall, 1884) is found along the coasts of Florida, northern Cuba, the Gulf of Mexico, Haiti, and the Yucatan Peninsula. Cernohorsky (1970) and Abbott (1974) synonymized *T. floridana* with *T. foveata*, before Maes and Raeihle (1975) demonstrated that they are separate species. These latter authors, following preliminary observations of Raeihle (1968), have shown in a detailed anatomical study of *T. floridana* that *Thala* belongs in the Costellariidae (as Vexillidae), and provided support for the then still controversial proposal that this latter taxon deserved full familial status apart from Mitridae (e.g., Azuma, 1965; Ponder, 1972) due to differences in gross anatomy and early life history.

In this work we describe a third western Atlantic species of *Thala* collected in beach sediments from Manati, Puerto Rico. Soft parts and radula are unknown; nonetheless, conchological characters are distinctive enough to justify the naming of a new species.

MATERIALS AND METHODS

Shells were measured using WILD M-5 and M-8 dissecting microscopes with ocular micrometers and photographed with a Nikon F2 camera with extension bellows and MicroNikkor 55 mm objective. Scanning electron micrographs were made using an ISI Double Stage DS-130 scanning electron microscope at the Electron Microscope Laboratory, Rosenstiel School of Marine and Atmospheric Science. Model I ANOVA with unequal sample sizes (Table 1) was performed according to Sokal and Rohlf (1981). Acronyms used throughout this paper are: ANSP, Academy of Natural Sciences of Philadelphia; FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Muséum National d'Histoire Naturelle, Paris; UF, Florida Museum of Natural History, University of Florida, Gainesville; UMML, Invertebrate Museum, University of Miami Rosenstiel School of Marine and Atmospheric Science; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

SYSTEMATICS

Family Costellariidae MacDonald, 1860
Genus *Thala* H. & A. Adams, 1853
Thala esperanza new species
(figures 1–6, Table 1)

Description: Shell fusiform (length/width ≈ 2.7), imperforate, reaching 5.0 mm in length, 1.9 mm width. Spire angle about 27°. Shell surface smooth, translucent, golden brown to chestnut brown, usually with single spiral band of lighter color on middle of last whorl. Periostracum undetectable. Protoconch usually decollated in adult shells, when present transparent brown, smooth, with 2 whorls, about 0.4 mm diameter, embryonic whorl

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Table 1. Linear shell measurements (mm) and counts for *Thala esperanza* new species, holotype and paratypes 1, 2, 5–12, and *T. foveata*. Statistics for model I ANOVA with unequal sample sizes according to Sokal and Rohlf (1981); NS = not significantly different.

Character	*T. esperanza* (n = 11)			*T. foveata* (n = 6)			ANOVA
	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	
Total length	3.92–5.00	4.40	0.40	5.25–6.33	5.73	0.40	$F = 24.14$ $p < 0.001$
Shell width	1.36–1.88	1.62	0.16	2.04–2.24	2.15	0.07	$F = 23.02$ $p < 0.001$
Length last whorl	2.80–3.48	3.17	0.22	3.72–4.28	3.97	0.19	$F = 56.34$ $p < 0.001$
Aperture length	1.92–2.44	2.18	0.15	2.84–3.32	3.02	0.20	$F = 81.54$ $p < 0.001$
Aperture width	0.36–0.60	0.49	0.06	0.64–0.80	0.71	0.05	$F = 65.12$ $p < 0.001$
Teleoconch whorls	3.25–5.00	4.18	0.45	4.00–4.75	4.42	0.26	NS
Spire angle (degrees)	26–29	26.9	1.14	35–37	36.0	0.89	$F = 213.9$ $p \ll 0.001$
Spiral cords last whorl	23–31	27.4	2.20	16–18	16.8	0.75	$F = 128.4$ $p \ll 0.001$
Axial ribs last whorl	24–32	28.3	2.65	21–27	23.0	2.28	$F = 23.41$ $p < 0.001$
Length/width	2.17–3.05	2.73	0.24	2.47–2.83	2.65	0.13	NS
Aperture length/total length	0.44–0.61	0.50	0.05	0.51–0.55	0.52	0.02	NS
Length last whorl/total length	0.65–0.87	0.72	0.06	0.66–0.71	0.69	0.02	NS
Aperture length/aperture width	3.78–4.58	4.27	0.24	3.55–4.87	4.26	0.51	NS

tilted, about 0.3 mm diameter. Protoconch/teleoconch transition orthocline. Teleoconch reaching 5 convex whorls. Suture impressed. Constriction present abapically at suture, defining a spiral cord wider than remaining spiral cords. Combination of spiral and axial elements producing clathrate aspect to entire teleoconch. Axial sculpture of 24–32 flattened ribs on last whorl. Interspaces as wide as axial ribs on early whorls, ¼ rib width on last whorl. Spiral sculpture of 23–31 cordlets on last whorl. Cordlets much narrower than axial ribs on early whorls, equal in width to axial ribs on last whorl. Five or six additional abapical spiral ribs at base slightly wider than those on remainder of last whorl. Aperture elongate (length/width ≈ 4.5). Outer lip with 9–13 small but well defined denticles that are absent in immature shells. Columella arched, with 4 columellar folds that follow orientation of spiral cords along base. Parietal region excavated, thus columellar plaits not raised above shell surface at base. Anterior siphonal canal wide, weakly defined. Posterior siphonal canal delineated only along inner surface of aperture, without notch.

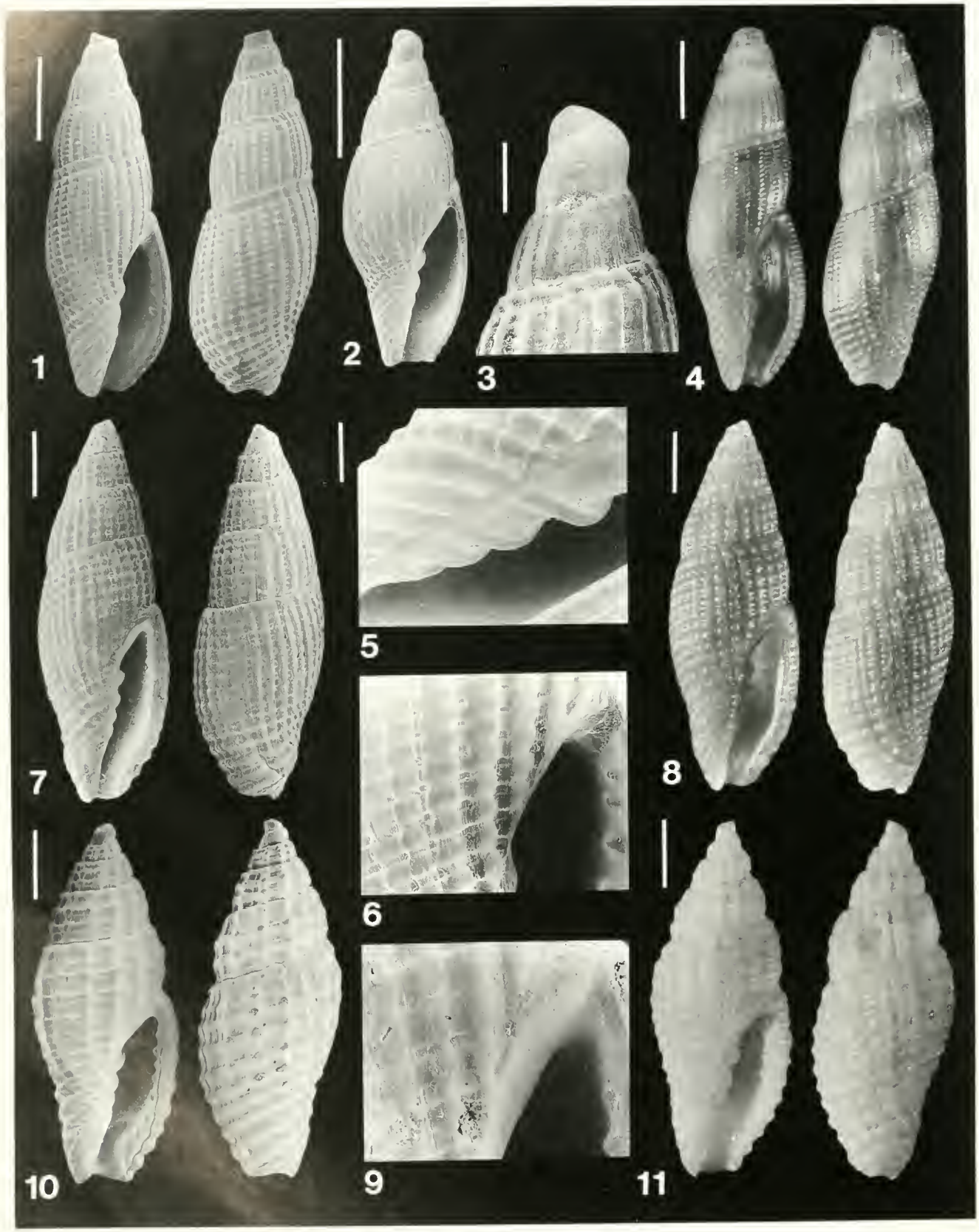
Holotype : USNM 860280, 5.00 mm length, 1.64 mm width.

Type locality: Playa Esperanza, about 40 km west of San Juan, Municipality of Manati, northern Puerto Rico.

Paratypes: Paratypes 1–4, USNM 860281; Paratypes 5–6, UF 193382-193383; Paratype 7, ASNP 391938; Paratype 8, AMNH 232313; Paratype 9, MCZ 302588; Paratype 10, MNHN, unnumbered; Paratype 11, FMNH 223388; Paratype 12, UMML 8375; Paratypes 13–16, USNM 860282; All from type locality, D. Piferer col. 05/1973, beach drift.

Remarks: Protoconchs are almost always decollated in beach-collected shells of this new species. Only two of 17 shells examined in this study had intact protoconchs, and those clearly were immature specimens. We do not know whether protoconch decollation occurs while snails are still alive. Decollation occurs frequently in unrelated gastropods (e.g., *Caducifer atlanticus* Coelho, Matthews & Cardoso, 1970, a buccinid from off Brazil, see Leal, 1991:151). The protoconch is very thin and translucent in *T. esperanza*. Decollation probably also occurs in *T. foveata*. In examining one of the specimens illustrated by Maes and Raeihle (1975) (UF 158165, St. Vincent, Lesser Antilles), we found that the protoconch of that specimen, present in Maes & Raeihle's illustration, is now missing (figures 7, 8).

Of the western Atlantic species of *Thala*, *T. esperanza* can be more easily separated from *T. floridana*. We do not provide statistical comparisons between these two species, but such comparisons may be made using data in Table 1 and in Maes and Raihle (1975). *Thala floridana* has a much thicker and larger shell, with nearly



Figures 1–6. *Thala esperanza* new species. **1.** Holotype, Playa Esperanza, Manati, Puerto Rico (SEM). **2.** Juvenile shell of paratype 4 (SEM). **3.** Protoconch of paratype 4 (SEM). **4.** Paratype 1. **5.** Parietal region showing columellar plaits on holotype (SEM). **6.** Shell sculpture near adapical part of aperture on holotype (SEM). All from type locality. **Figures 7–9.** *Thala foveata*, UF 158165,

twice the average width of *T. esperanza*. Shells of *T. floridana* are usually dark brown, but some can be white (Maes & Raeihle, 1975) (figure 11). Shells are never white in *T. esperanza*. The 40° spire angle of *T. floridana* is broader than that of *T. esperanza* (27°). *Thala floridana* has a much coarser sculptural pattern (figures 10, 11), with about 13 spiral cords and 20 axial ribs on the last whorl. These numbers average 27.4 and 28.3, respectively, in *T. esperanza* (figures 1, 4, Table 1) (See Appendix 1 for a list of specimens of *Thala floridana* examined).

The degree of overall shell similarity between *T. esperanza* and *T. foveata* is greater. Table 1 shows measurements, proportions, and meristic counts for adult shells of the two species. All known specimens of *T. foveata* are thicker and significantly larger (Table 1) than any shell in the type series of *T. esperanza*. The base in *T. foveata* is always more tapered. *Thala esperanza* differs in having flattened axial ribs with narrower interspaces, significantly larger spire angle, and greater numbers of spiral cords and axial ribs on last whorl. There is also a marked, distinctive constriction defining a wider spiral cord just below the suture in the new species (figures 1, 4, 7, 8) (See Appendix 1 for specimens of *T. foveata* examined).

Thala esperanza can be distinguished from its eastern and western Pacific congeners by its much smaller size and differences in shell shape and sculpture. *Thala gratiosa* (Reeve, 1845) from tropical west America has a somewhat similar shell contour, but is twice as large and has a much coarser sculpture with relatively fewer elements (Keen, 1971; Sphon, 1969). The western Pacific *T. milium* (Reeve, 1845) and *T. todilla* (Mighels, 1845) also differ by their larger size, coarser sculpture, purple color in the former and four-whorled protoconch in the latter (Cernohorsky, 1970; Kay, 1979).

ACKNOWLEDGEMENTS

We thank D. Prinez for making available all specimens of the type series. Loans of material for comparison were provided by F.G. Thompson and K. Auffenberg (UF), S.P. Kool (MCZ), G. Rosenberg (ANSP), W.K. Emerson and W.E. Sage (AMNH), and M.G. Harasewych (USNM). We are also indebted to M.G. Harasewych and to an anonymous reviewer for criticisms that helped improve the manuscript. N.A. Voss and P.L. Blackwelder allowed for use respectively of the facilities at the Invertebrate Museum and Electron Microscopy Laboratory, RSMAS, University of Miami.

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APPENDIX 1

Material of *Thala foveata* examined, all from Calliaqua, St. Vincent, British Virgin Islands: UF 158165, 1 shell, beach drift, H.H. Monroe, 01/1961, ex-McGinty Collection; UF 145855, 2 shells, H.H. Monroe, 01/1961, ex-McGinty Collection; "rocky cove on windward side of SE Point, Calliaqua Bay", 13°07′20″N, 61°11′55″W, ANSP 324791, 1 shell, V.O. Maes 02/1972; 13°07′04″N, 61°12′20″W, ANSP 354555, 2 shells, H.H. Monroe 1956, Ex-Finlay Collection.

Material of *Thala floridana* examined: East Coast of Florida: St. Augustine, UF 158167, 3 shells, Ted Yocius 10/1972, 225 ft, Ex-J.M. Bijur Collection; AMNH 246013, 2 shells, Ted Yocius, Jerome M. Bijur Collection; Fort Pierce, AMNH 127640, 16 shells, Thomas Hughes leg.; MCZ 298862, 3 shells, Bernadine Baker coll., Ex-Doris Folsom 5/1976; Palm Beach, Boynton Beach, UF 145856, 1 shell, McGinty 8/1944; UF 169469, 41 shells, McGinty Collection, 02/1944; Boynton Beach, Ocean Ridge, UF

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St. Vincent, West Indies. **7.** Shell (SEM). **8.** Shell. **9.** Shell sculpture near adapical part of aperture (SEM). **Figures 10–11.** *Thala floridana*. **10.** USNM 860284, Bear Cut, Miami, Florida (SEM). **11.** USNM 860283, off Miami Beach, Florida. Scale bars = 1 mm, except for Figures 3, 5, 6, 9 = 0.2 mm.

158164, 1 shell, T. McGinty 8/1944; Card Sound, UF 63207, 2 shells, M. Smith 1/1935, University of Alabama leg.; UF 13150, 1 shell, C.B. Lungren 1909; 1.6 km off Miami Beach, USNM 860283, 1 shell, M. Almasi and D. Marszalek 10/1978, 24 m depth; Bear Cut, Miami, USNM 860284, A. Emery 02/1956, beach drift; Bird Key, Biscayne Bay, UNSM 414387, 3 shells, *Eolis* Sta. 13, 2–10 ft., Henderson Coll. 1910; Florida Keys: Key Largo, AMNH 242626, 4 shells, ex-Alice Denison Barlow Collection; Little Molasses Reef, off Key Largo, UF145851, McGinty 4/3/1950; Bonefish Key, UF 192101, 4 shells, Beal-Maltbie coll., Ex-McGinty Collection; UF 146530, 1 shell, McGinty Collection; UF 63202, 8 shells, M. Smith coll., University of Alabama leg.; UF 162451, 3 shells, Blenn R. Bales, G.L. Warmke leg. 1989; UF 135603, 3 shells, V. Orr, H.G. Lee leg.; MCZ 118844, 10+ shells, B.R. Bales 5/7/1940; MCZ 100714, 8 shells, B.R. Bales leg.; AMNH 116412, 2 shells, 1940, Dr. and Mrs. Julius Wisoff Collection; AMNH 114121, 1 shell, T. McGinty coll.; AMNH 138995A, 1 shell, A.S. Koto leg.; AMNH 189020, 4 shells, A.S. Koto leg. 1949, J.M. Cate Collection; AMNH 138995, 4 shells, A.S. Koto leg., M.K. Jacobson Collection; AMNH 199169, 9 shells, A.S. Koto leg.; Lower Matecumbe Key, USNM 53477, 3 shells, H. Hemphill, in grass; Key Vaca, UF 156266, 9 shells, McGinty 2/1939; MCZ 153269, 25+ shells, B.R. Bales; Key Vaca, Boot Key Harbor, UF 145853, 7 shells, McGinty coll. 3/1945; MCZ 226804, 2 shells, grassy bottom, 1 fm. McGinty coll.; No Name Key, UF 63203, 2 shells, University of Alabama leg.; Little Torch Key, UF 123072, 33 shells, M.C. Teskey 1968-1977, on sand patches; Grassy Key (Florida Bay), MCZ 110198, 4 shells, under rocks, P. McGinty leg.; Pumpkin Key, UF 63205, 2 shells, M. Smith 1/1935, University of Alabama leg.; Islamorada, AMNH 121444, 3 shells, ex-E.C. Styles; Big Pine Key, UF 63204, 4 shells, M. Smith coll., University of Alabama leg.; Key West, AMNH 8982, 3 shells, Constable, Jay Collection; USNM 53541, 1 shell, H. Hemphill, on rocks; Barraconta Key, 9 miles W of Key West, UF 13149, 2 shells, G.W. Van Hyning, 6/11/1958; Middle Sambo Shoals, UF 145852, 6 shells, McGinty 6/1946; Dry Tortugas: MCZ 258469, 1 shell, J.S. Schwengel, dredged; Loggerhead Key, UF 158168, 1 shell, T. McGinty 8/1941, 0.5 fm; Garden Key, South Coaling Dock, UF 13151, 2 shells, G.W. Van Hyning 7/16/1938, on piling; Gulf Coast of Florida: St. Martins Reef, near Aripeka Bird Racks, 6 mi. W of Aripeka, Pasco-Hernando County line, MCZ 233672, 14 shells, W.A. Smith 5/25/1963; Ozone, Crystal Beach, AMNH 246038, 3 shells, Dan Steger coll., Jerome Bijur Collection; AMNH 125612, 10 shells, S. Levine leg. 1960; AMNH 189024, 5 shells, S. Levine leg. 1960, J.M. Cate Collection; AMNH 125928, 76 shells, S. Levine leg. 1960; AMNH 194560, 66 shells, Gordon Newell-Usticke Collection; Ozone, Crystal Beach, St. Joseph Sound, UF 193036, 27 shells, Dan Steger; UF 137573, 5 shells, D. Steger 1970, H.G. Lee leg.; AMNH 189023, 3 shells, mud and grass bottom, E. Marcott leg. 1963, J. Cate Collection; Marco, UF 137649, 1 shell, H. Hemphill, 2 fms, H.G. Lee leg.; USNM 53542, 1 shell, H. Hemphill; 15-35 mi. off Ft. Walton (FL), MCZ 145877, 5 shells, 13–19 fms., L.A. Burry; Featherbend Bank, UF 63206, 2 shells, M. Smith 1/1935, University of Alabama leg; Okaloosa County, off Destin, UF 158166, 1 shell, UF 145857, 2 shells, McGinty 10/1941, 14 fms; Bahamas: Andros, first island off Mintie Bar, SE end of South Bight, USNM 271832, 7 shells, P. Bartsch; Abaco, Little Harbor, USNM 180492, 5 shells, O. Bryant; Grand Bahama Island: Dead Man's Reef, 26°34′45″N, 78°51′45″W, ANSP 371266, 1 shell, J. Worsfold, Ex-J. Worsfold; McLean's Town, 26°38′45″N,77°57′30″W, ANSP 369060, 8 shells, J. Worsfold, Ex-J. Worsfold; Eight Mile Rock, Hepburn Town, "Garbage Hole", 26°31′30″N, 78°47′15″W, ANSP 370392, 4 shells, J. Worsfold, Ex-J. Worsfold; Wood Cay, 26°44′15″N, 79°58′15″W, ANSP 369615, 3 shells, J. Worsfold, Ex-J. Worsfold; West End, Settlement Point, 26°42′15″N, 78°59′50″W, ANSP 368626, 6 shells, J. Worsfold, Ex-J. Worsfold; West End, Hotel Jetty, 26°42′15″N, 078°59′50″W, ANSP 368711, 21 shells, J. Worsfold, Ex-J. Worsfold; Nassau, New Providence Island, UF 145849, 1 shell, McGinty 6/6/1947, 4–6 fms, Sta. 17; Cuba: Las Villas, Caibarien, Cayo Salinas, AMNH 138924, 1 shell, M.K. Jacobson leg., 07/1947; Esperanza (NW Cuba), USNM 414396, 5+ shells, Barrera Expedition, Sta. 210, 2–3 fms; Santa Rosa (NW Cuba), USNM 414498, 1 shell, Barrera Expedition, Sta. 209, 3-6 fms; Bermuda, AMNH 45068, 2 shells, Constable, Jay Collection; MCZ 24174, 2 shells, O. Bryant 1903; USNM 223283, 6 shells, Haycock coll.; Haiti, Dept. de l'Ouest, Saltrois, USNM 439975, 1 shell, Orcutt, Chamberlain Coll.

Shell and Pallet Morphology of Early Developmental Stages of *Bankia gouldi* (Bartsch, 1908) (Bivalvia: Teredinidae)

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ABSTRACT

The margin of the larval shell of *Bankia gouldi* (Bartsch) undergoes a progressive change in shape during ontogeny from an initial D-shape, to nearly circular, and then to elliptical just prior to metamorphosis. The length of the hinge is 37.9 ± 2.3 μm, n = 30 (range: 34.0–43.0 μm). The D-stage larval shell is inequilateral with the anterior end broader than the posterior end. The provinculum, composed of two cardinal teeth and three sockets in the left valve, and three cardinal teeth and two sockets in the right valve, is well developed in shells as small as 75 μm. The length of the central tooth in the right valve ranges from 12 to 19μm. The other teeth are one-half to one-third of the length of the central tooth. A lateral hinge system, consisting of two lateral flanges on the left valve that interlock with two lateral grooves on the right valve, is present in specimens as small as 75 μm. This hinge system persists until metamorphosis. Metamorphosis, first seen in the development of a ligament pit, occurred in larvae with shells as small as 197 μm in height; and leads to the development of the chondrophore, apophysis, anterior and posterior slopes, disc, umbonal-ventral ridge, dorsal condyle, ventral condyle, denticulated ridges and pallets. Asymmetrical growth results in the formation of the characteristic form of the teredinid postlarval shell with a new axis of articulation oriented dorsoventrally along the condyles. Each pallet consists of a proximal stalk and a distal blade with one to several segments. Pallets with one segment were first observed in early postlarval shells at 0.4 mm in length.

Key words: larvae, postlarvae, shell morphology, Teridinidae, metamorphosis.

INTRODUCTION

Morphological classification schemes used in the identification of bivalve larval stages have been developed from light microscopic examination of plankton (Jorgensen, 1946; Rees, 1950) or cultured larvae (Loosanoff *et al.*, 1966; Chanley & Andrews, 1971). More recently, the scanning electron microscope (SEM) has enabled workers to describe in detail the hinge and other minute structures of bivalve larvae and postlarvae that are useful in species identification (Turner & Boyle, 1975; Carriker & Palmer, 1979; Chanley & Dinamani, 1980; Le Pennec, 1980; Lutz *et al.*, 1982a, b; Lutz, 1985; Prezant, 1990; Waller, 1991). A method of consistently orienting and documenting the shapes and dimensions of larval shells (Lutz *et al.*, 1982b; Fuller *et al.*, 1989b) has provided an additional means of differentiating bivalve species. The present manuscript is part of an ongoing effort to document the gross morphology, hinge apparatus and other morphometric features of larval and early postlarval shells of bivalve mollusks to facilitate taxonomic identification of individual specimens to the species level (Fuller & Lutz, 1989a; Fuller *et al.*, 1989c; Kennedy *et al.*, 1991; Goodsell *et al.*, 1992; Gustafson & Lutz, 1992).

Bankia gouldi (Bartsch, 1908) is an oviparous mollusean woodborer found in tropical and temperate waters of the western Atlantic Ocean (Turner, 1971). As an adult, *B. gouldi* has a soft, vermiform body, a diminutive shell that covers the anterior-most portion of the body, and segmented pallets situated at the base of the siphons beneath a muscular collar (Turner, 1966, 1971). The pallets are not formed until after metamorphosis and, therefore, are of no value in identification of larval shells. In addition, previous descriptions of the larval shell, early postlarval shell and pallet of *B. gouldi* are insufficient to allow congeneric differentiation. Hence, a means of identifying younger specimens of *B. gouldi* is clearly needed. This work presents both qualitative and quantitative data on the morphology of the larval shell, early postlarval shell and pallet of *B. gouldi* that can aid in species identification of early ontogenetic stages. In particular, we show that the following features are important in distinguishing the larvae of *B. gouldi* from *T. navalis*: slope of the shoulders, length of provinculum/hinge-line, and length of posterior tooth of the left provinculum.

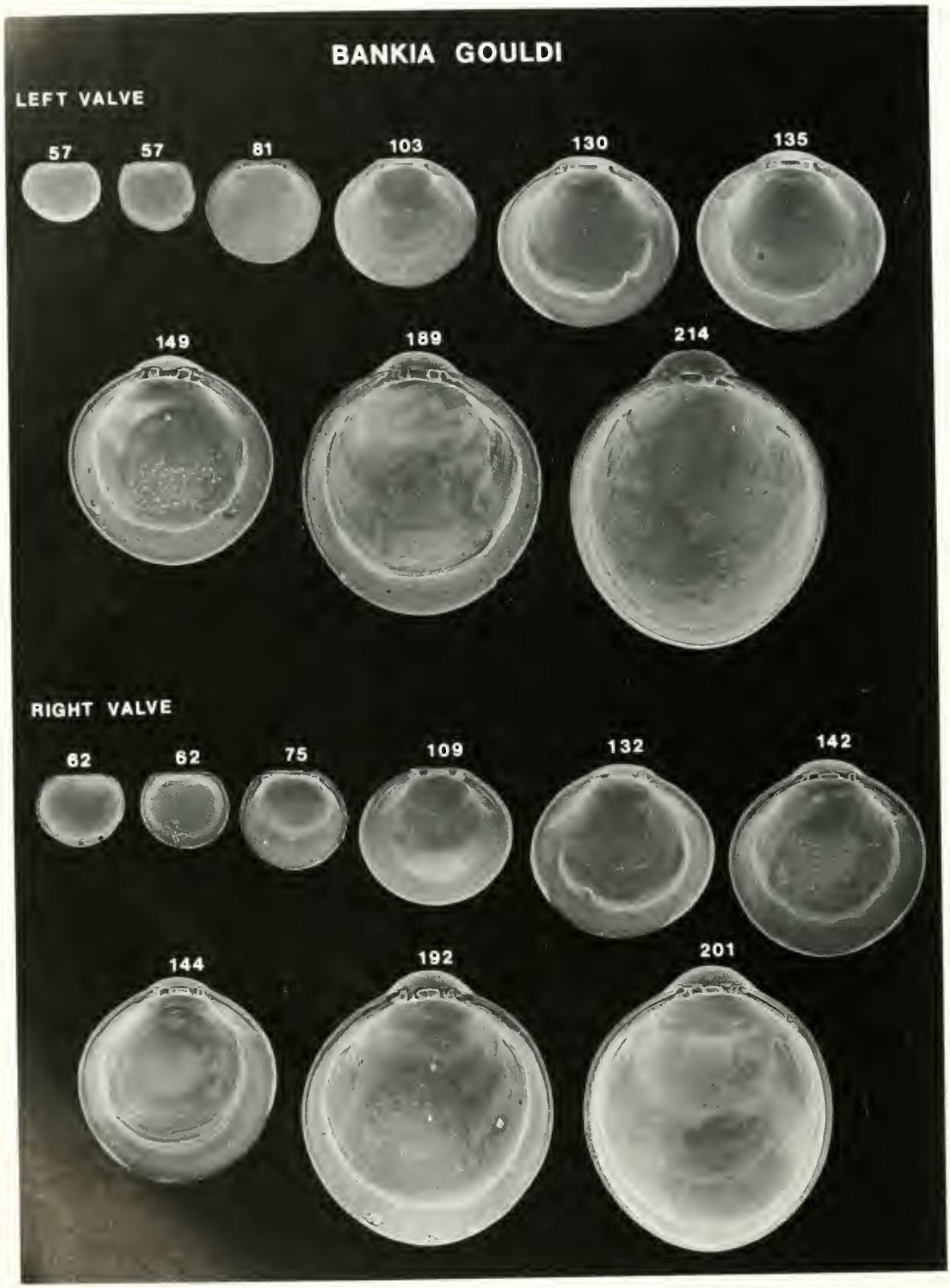

Figure 1. Internal surface view of disarticulated larval shells. Anterior end of the left valve is oriented towards the right, whereas the anterior end of the right valve is oriented towards the left. The number above each valve signifies the maximum linear shell dimension in μm.

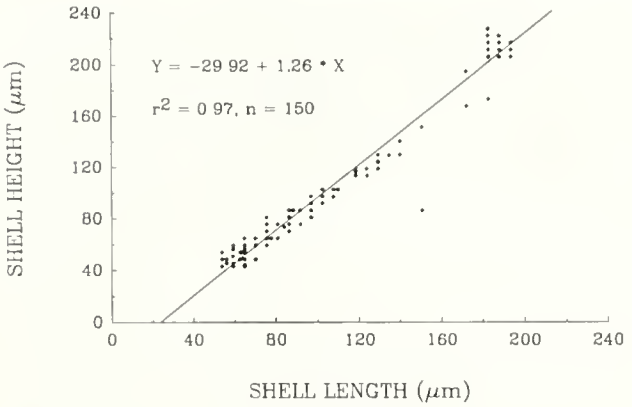

Figure 2. Linear regression of shell height plotted against shell length of larvae.

Table 1. Dimensions in μm of the larval shell of *Bankia gouldi* shown in Figures 1 and 2. 1 SD = one standard deviation.

	Range	Mean ± 1 SD	Sample size
Left Valve			
Anterior tooth length	7.5–9.4	8.3 ± 0.8	7
Posterior tooth length	5.5–7.1	6.4 ± 0.6	7
Provincular length	36.0–40.5	38.1 ± 1.8	9
Right Valve			
Anterior tooth length	3.9–4.9	4.5 ± 0.4	8
Central tooth length	12.5–15.5	14.5 ± 1.2	7
Posterior tooth length	4.5–5.9	5.0 ± 0.5	9
Provincular length	34.0–40.5	37.8 ± 1.9	9

MATERIALS AND METHODS

Specimens of *Bankia gouldi* were collected from wooden frames of trays set out for a year in the York River at Gloucester Point, VA by Dr. Mary Gibbons. Adults were mass spawned, and the fertilized eggs were grown to the early adult stage using standard techniques (Loosanoff & Davis, 1963; Castagna & Kraeuter, 1984). The temperature of the culture water ranged from 22 to 30°C, and salinity, from 32 to 34 ppt salinity. Floating blocks of wood were provided as substrata for metamorphosing larvae. Larvae and postlarvae were sampled regularly and preserved in 95% ethanol. The preparation of specimens for SEM examination was described previously by Fuller *et al.* (1989b). The specimens were coated with about 600 Å gold-palladium using a Polaron Coating Unit E5100, and they were examined using a Hitachi-450 SEM. Calibration of orthogonality of the SEM was done with the aid of metallic spheres or glass microspheres. Dimensions in the SEM were calibrated using a calibrated ocular micrometer, a glass microsphere, or a grid of known dimension. Specimens were prepared, consistently oriented, and photographed as previously described to facilitate comparison of shapes and measurements (Lutz *et al.*, 1982b; Fuller *et al.*, 1989b, c). Shell terminology is described in Rees (1950), Turner (1966), Chanley and Dinamani (1980), and Fuller *et al.*, (1989c).

The maximum linear dimension, shell length, shell height, provincular length, tooth length and the lateral hinge length were measured from calibarated scanning electron micrographs of oriented shells. The shell height and length of the shell, hinge line and pallet were also measured using a compound microscope with the same calibrated ocular micrometer used to calibrate the scale of the SEM. These terms are defined in Fuller *et al.* (1989c).

Whenever possible, we compared our results quantitatively with previously published data. Variables that changed with growth were compared using analysis of covariance, whereas variables that were independent of size were compared using the Student t-test, Tukey, or Student-Neuman-Keuls multiple range test (Zar, 1984).

The larval shells in Figures 1 and 3 are referred to by their maximum linear shell dimension, which is the greatest distance between two points on a contour of a valve oriented in a standard fashion as described previously. The early postlarval shells in Figures 5–7 are referred to by their shell height. Numbers separated by a slash (e.g. 57/62) indicate left and right valve dimensions respectively.

RESULTS

Larval shell: One day after fertilization the shell length was 61.1 ± 4.5 μm, n = 30 (range: 54–70 μm); shell height was 49.3 ± 4.5 μm, n = 30 (range: 43–59 μm); hinge line/provincular length was 37.9 ± 2.3 μm, n = 30 (range: 34.0–43.0 μm). Most valves of the straight-hinge larvae are inequilateral with the anterior end broader and protruding farther beyond the hinge line than the posterior end (Fig. 1, 57/62).

The larval shell undergoes gradual allometric changes during ontogeny from a D-shape, to a nearly circular shape, and finally to an elliptical shape just prior to metamorphosis (Fig. 1). During larval growth the maximum shell dimension shifts from an anteroposterior to a dorsoventral axis. Larval shells are almost equidimensional (length = height) at approximately 143 μm (Figs. 1, 2).

The relationship between the length and height of the larval shell is described by the equation, $Y = -29.92 + 1.26X$ ($r^2 = 0.97$, n = 150), where Y = height and X = length in μm (Fig. 2). A second power polynomial equation (quadratic equation) fits the data points only slightly better than the linear regression equation.

The provinculum consists of two cardinal teeth and three sockets on the left valve that interlock with three cardinal teeth and two sockets on the right valve (Figs. 1, 3). The onset of provincular development is variable, occurring at about 57 μm. An individual at 57 μm can be in the prodissoconch I stage without any trace of a provinculum, or in the early prodissoconch II stage with a developing provinculum (Fig. 3, 57 μm). Development of the provincular teeth in the right valve starts with the formation of the posterior tooth, followed by formation

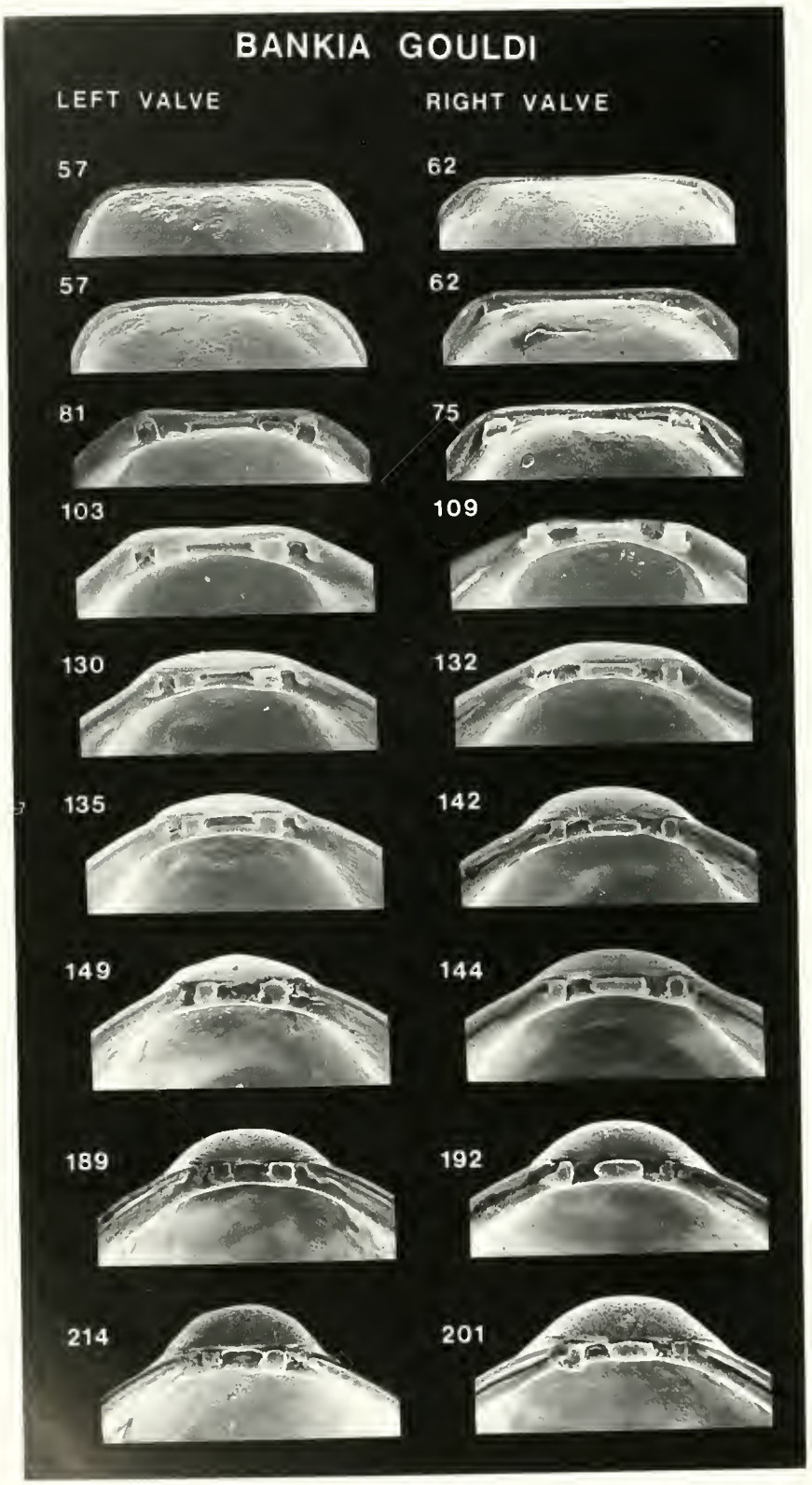

Figure 3. Scanning electron micrographs showing hinges of larval shells seen in Figure 1.

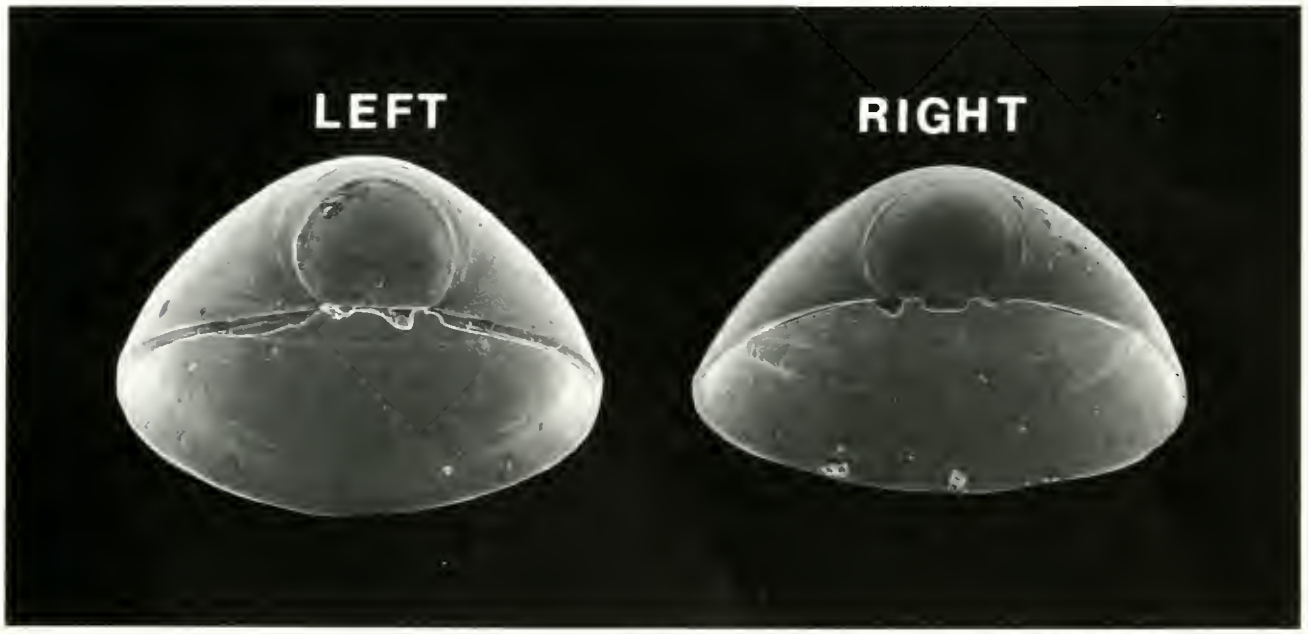

Figure 1. Dorsomedial view of the larval shells. Orientation as in Figure 1. The lateral hinge system consists of two lateral flanges on the left valve and two lateral grooves on the right valve on each end of the provinculum. Horizontal valve width: left = 198 μm; right = 185 μm.

of the anterior tooth, and culminating with the formation of the central tooth (Fig. 3, 62 μm, 75 μm). The provinculum is well-developed in valves measuring 75 μm.

The longest provincular tooth is the central one, which can reach 19 μm. The other teeth are either one-half or one-third of the length of the central tooth (Table 1). The left anterior tooth is consistently larger than the left posterior tooth, but the right anterior and right posterior teeth are not consistently different in size (Figs 1, 3). The increase in tooth length relative to shell length is variable: the total provinculum increases more slowly on the right valve than on the left valve. Only the length of the left anterior tooth regressed against shell length during growth was significant ($r^2 = 0.57$, Table 2), others were not. The provincular length measured from scanning electron micrographs agrees with the hinge-line length values of articulated valves measured by a light microscope.

Lateral flanges and grooves are present in valves as small as 75 μm (Figs. 1, 3), and persist until metamorphosis. Two lateral flanges on the left valve (Fig. 1, 81–214 μm, Fig. 4) interlock with the two lateral grooves on the right valve (Fig. 1, 75–201 μm, Fig. 4). Each lateral flange or lateral groove extends from the ends of the provinculum for about 1/10–1/15 of the perimeter along the dorsal commissure of the larval shell (Figs. 1, 4). The length of the anterior and posterior lateral grooves are equal in shells up to 109 μm (Fig. 1), but in larger valves the anterior lateral groove increases in size reaching a length up to 12% greater than that of the posterior lateral groove (Figs. 1,4).

Early postlarval shell: The first morphological evidence of metamorphosis is the development of a ligament pit beneath the posterior tooth and socket in valves measuring 235/230 μm in height (Figs. 5, 6). After metamorphosis, the growth of the postlarval shell is very asymmetrical (Figs. 5, 7, 8). The postlarval shell is slightly inequivalve, with the right valve longer than the left valve (Fig. 8). The ventral margin of the right valve is narrower than that of the left valve. The denticles on the denticulated ridge are predominantly two pronged, with the dorsal prong larger than the ventral prong. The ventral margin grows faster medially than the anterior shell margin, while the growth of the posterior margin lags behind (Figs. 5, 7, 8). The length to height ratio of

Table 2. Linear regressions of the shell height, tooth length or provincular length plotted against shell length of *Bankia gouldi* shown in Figure 1. a = intercept, b = slope, r^2 = coefficient of determination, P = probability of the regression coefficient (slope) of each regression, N = sample size.

Dependent Variable	a	b	r^2	P	N
Left Valve					
Shell height	−31.42	1.27	0.98	<0.01	9
Anterior tooth	5.88	0.02	0.57	0.05	7
Posterior tooth	6.66	−0.002	0.02	0.76	7
Provinculum	37.32	0.01	0.03	0.65	9
Right Valve					
Shell height	−27.57	1.22	0.98	<0.01	9
Anterior tooth	4.89	−0.003	0.14	0.35	8
Central tooth	12.71	0.01	0.18	0.35	7
Posterior tooth	5.36	−0.003	0.09	0.43	9
Provinculum	42.13	−0.04	0.71	<0.01	9

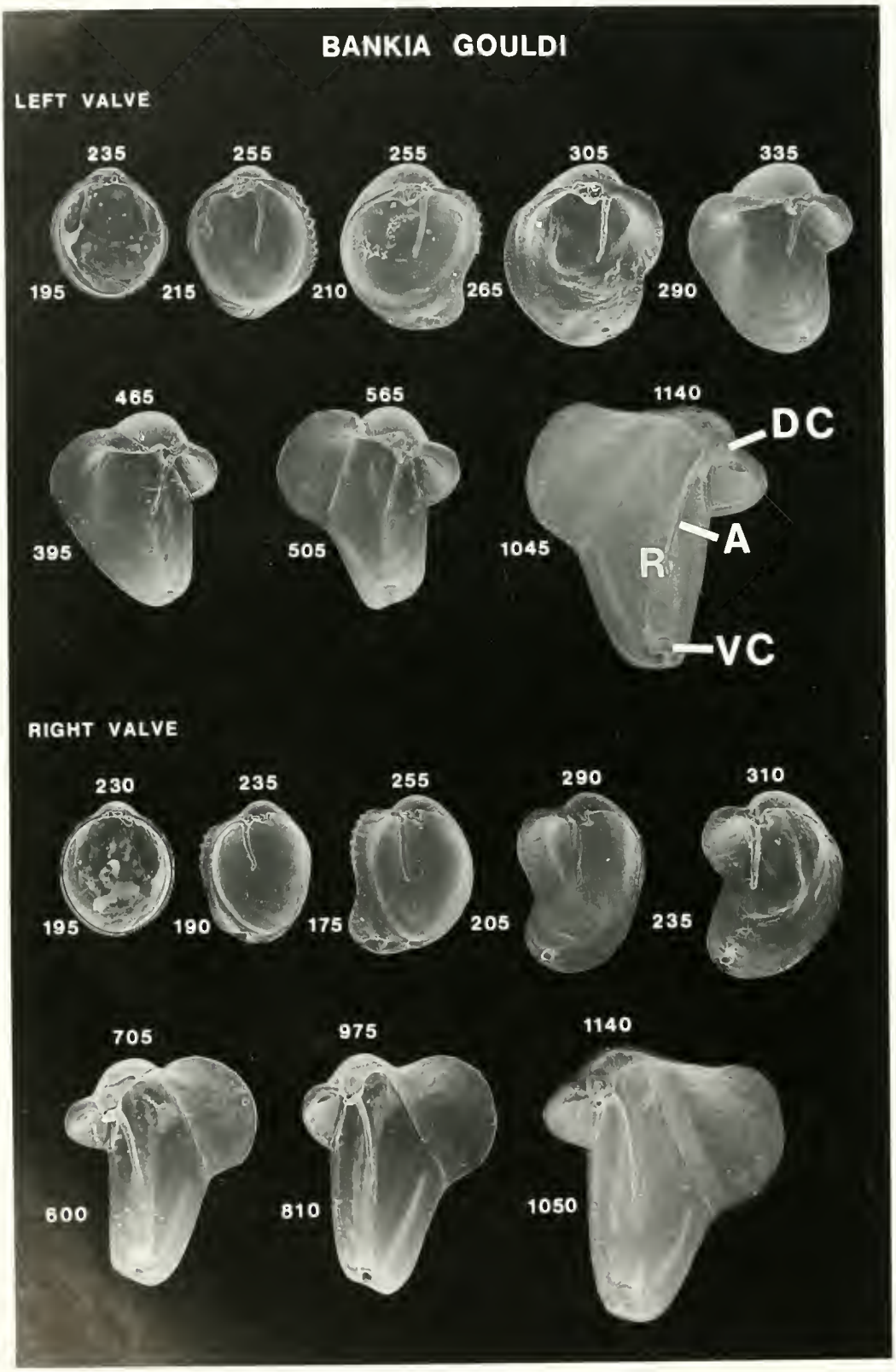

Figure 5. Internal surface view of early postlarval shells. Orientation as in Figure 1. The number above each valve signifies the shell height measured in μm roughly perpendicular to the hinge region. The number on the lower left of the valve is the shell length in μm measured roughly parallel to the hinge region. A = apophysis, DC = dorsal condyle, VC = ventral condyle, R = umbonal-ventral ridge.

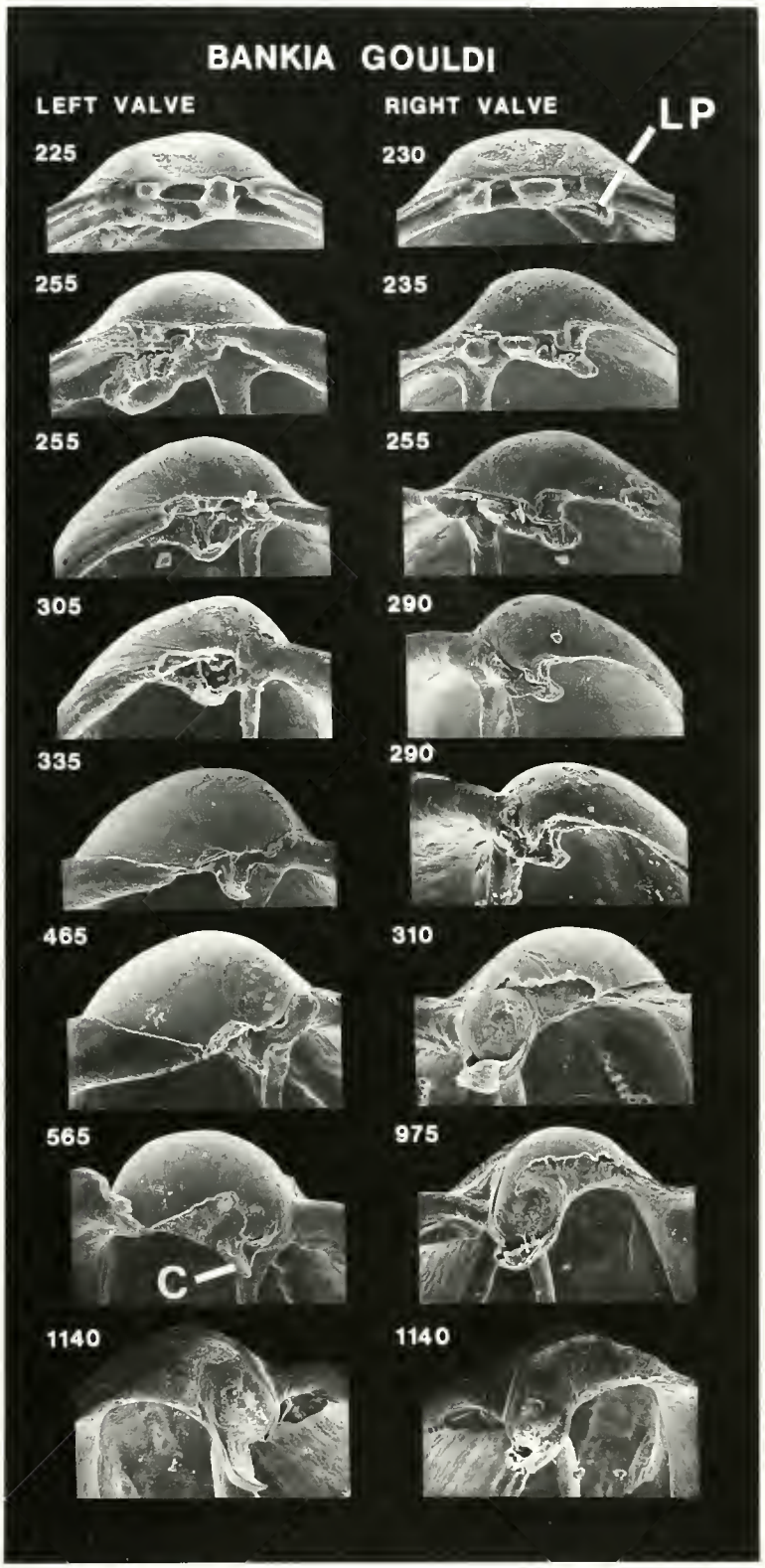

Figure 6. Scanning electron micrographs of the hinge region of early postlarval shells seen in Figure 5. The number above each valve signifies shell height in μm. LP = ligament pit, C = chondrophore.

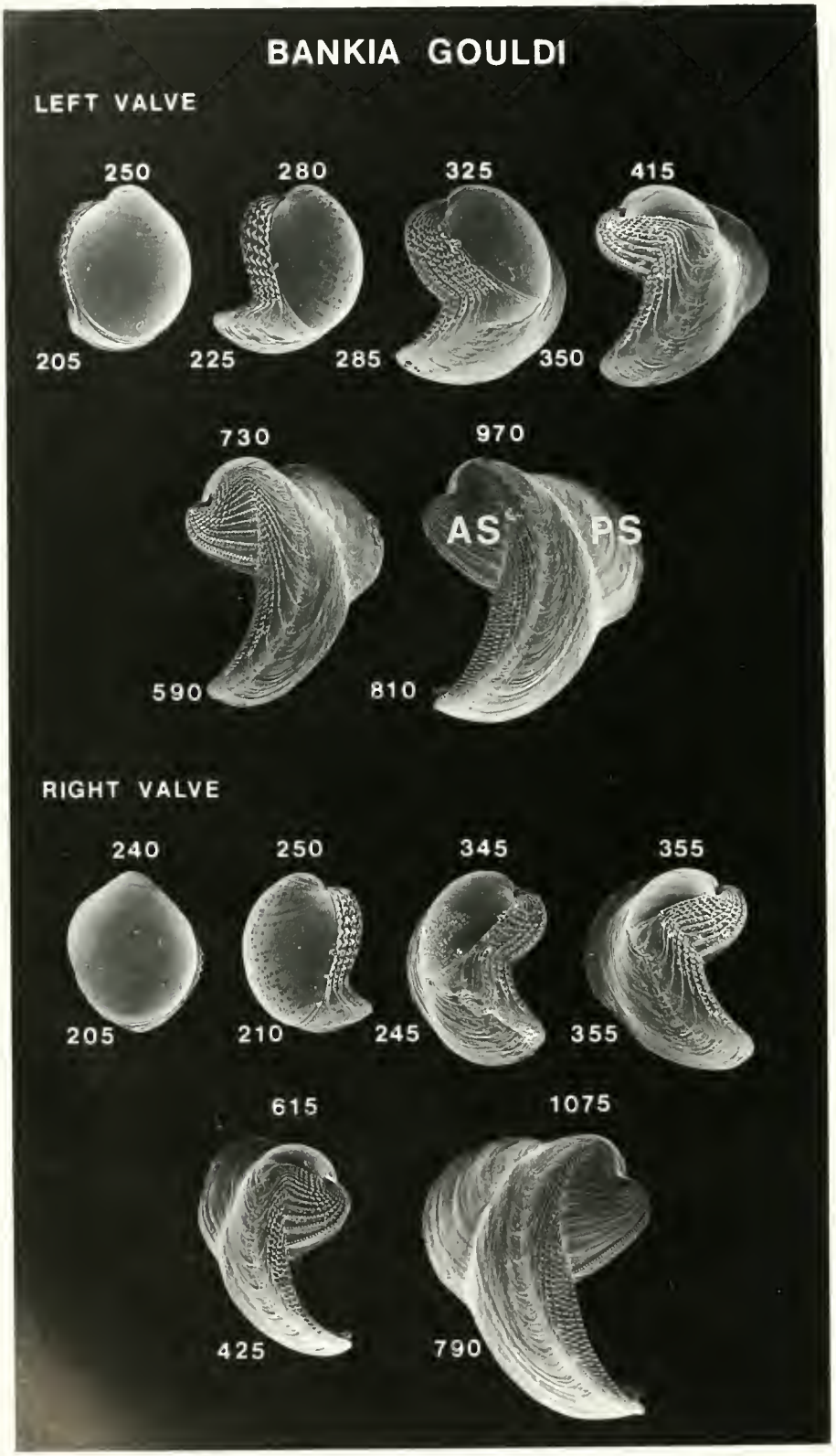

Figure 7. Scanning electron micrographs of the external surface of early postlarval shells. Orientation and number representation as in Figure 5. AS = anterior slope, PS = Posterior slope.

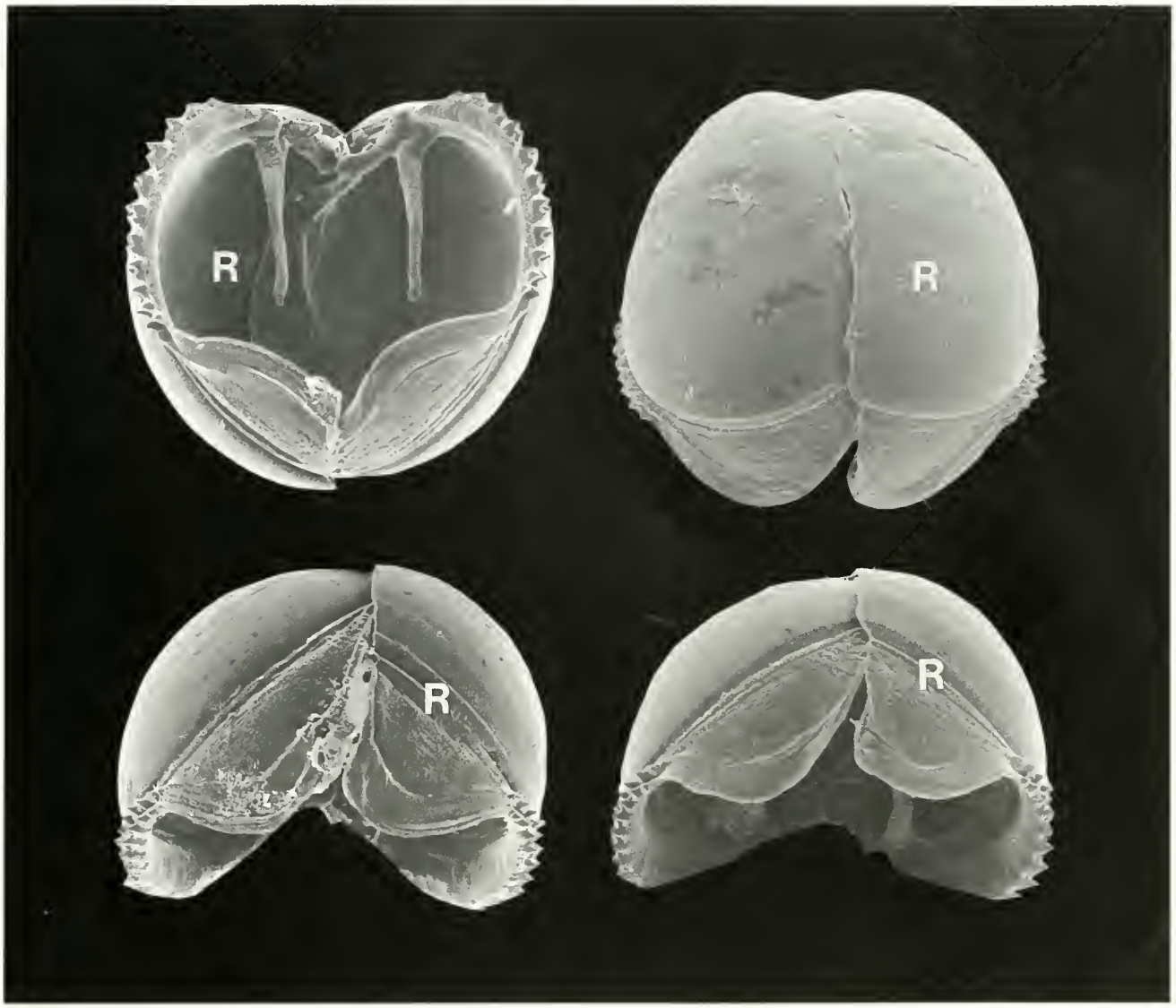

Figure 8. Views from different directions of partially articulated early postlarval shells with two denticulated ridges. The anterior (top left) and the posterior (top right) views show that the right valve (R) is slightly longer than the left valve. The ventral view at the bottom shows that the ventral margin of the right valve is narrower than that of the left valve. Most teeth have two prongs. The dorsal prong of the tooth is larger than the ventral prong. Horizontal valve widths are as follows: top left valve = 235 μm, top right valve = 243 μm, bottom left valve = 225 μm, bottom right valve = 239 μm

the postlarval shell continues to decrease with growth (Figs. 9).

The chondrophore that forms at the base of the posterior tooth and socket grows anteroventrally then medially, assuming a recurved formation (Figs. 5, 6). A saber-like apophysis develops beneath the anterior tooth and socket, and elongates along the sagittal plane in a posteroventral direction (Figs. 5, 6 height 255/235 μm). The dorsal portion of the posterior slope and the anterior slope are reflected up and outward (Figs. 5, 6, height 305–1140/290–1140 μm). The base of the apophysis and the adjacent reflected part of the anterior slope and umbo are incorporated to form the dorsal condyle (Figs. 5, 6, height 305–1140/290–1140μm). The enlarged chondrophore and dorsal condyle eventually conceal the provinculum. As growth proceeds, the ventral portion of the disc and the anterior slope curves ventromedially (Figs. 5, 7, 8). The shell thickening at the medial side of the ventral margin eventually develops into the ventral condyle (Fig. 5, height 255/235μm). An umbonal-ventral ridge, extending from the larval shell to the ventral condyle, forms on the inner shell surface (Fig. 5, height 335–1140/705-1140μm). The umbonal-ventral ridge is visible as an umbonal-ventral sulcus on the external shell surface (Fig. 7, 415–970/355–1075 μm). The posterior slope (auricle) overlaps the disc forming the shelf. The asymmetrical growth of the shell eventually results in the formation of the characteristic form of the teredinid

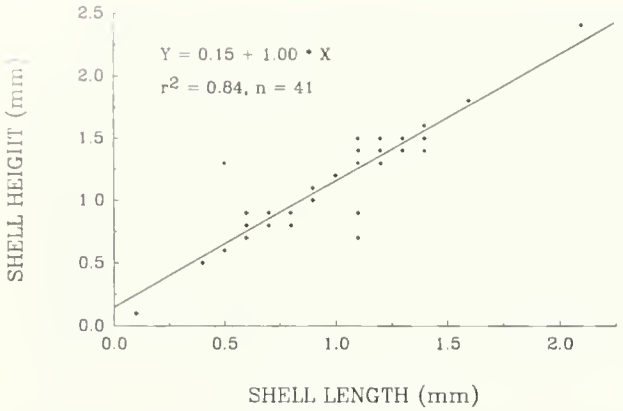

Figure 9. Relationship between shell length and shell height of early postlarval shells.

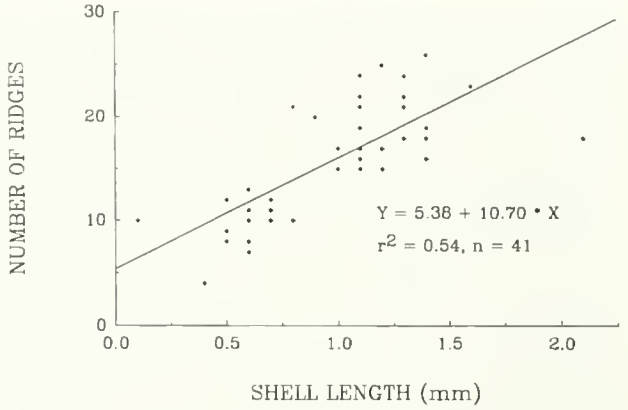

Figure 10. Relationship between shell length and number of denticulated ridges on the exterior surface of early postlarval shells.

postlarva, with the axis of articulation changing from an anteroposterior to a dorsoventral orientation along the condyles.

Early in the formation of the postlarval shell, denticulated ridges are added onto the anterior margin of the shell, initially only on the anterior area of the anterior slope (Fig. 7, height 250–280/240–250 μm). As the shell grows larger, the denticulated ridges extend to the anterior median area of the anterior slope. The number of denticulated ridges increases significantly with the increase in shell length; regression equation, $Y = 5.38 + 10.7X$, ($r^2 = 0.54$, $n = 41$), where Y = number of ridges and X = shell length in millimeters (Fig. 10).

Pallet: A one segment pallet was present at a shell length of 0.4 mm; at a shell length of 1.2–1.3 mm, the pallet had 13 segments. The pallet consists of a proximal stalk and a distal blade with one to several segments (Fig. 11), with the basal pallet segment being the largest. The angle formed by the base of the blade and the stalk is larger on the dorsal than the ventral side. The medial inner wall of the blade is flat, while the shorter outer wall of the blade is convex. The plane circumscribed by the distal outer margin of the blade is tilted anteriorly such that the distal border of the inner margin extends further posteriorly. Each pallet appears hemispherical when viewed from the distal end. The left and right pallets in an individual are morphologically similar and have the same number of segments (Fig. 11, height 250–505 μm), whereas pallets with the same number of segments from different individuals can vary in form (Fig. 11, height 840–1415 μm).

DISCUSSION

Larval shell: *Teredo navalis* Linnaeus, 1758 is the only other teredinid species whose larval and postlarval shell morphology has been oriented and photographed in a consistent manner (Fuller *et al.*, 1989c). In larval shells of similar size, the shoulders of *T. navalis* (Fig. 1, Fuller *et al.*, 1989c) are considerably steeper (less rounded) than those of *Bankia gouldi* (Fig. 1). The shoulders refer to the dorsal shell margin on the anterior and posterior ends of the hinge (Chanley & Dinamani, 1980). This difference in larval shell shape can be used to distinguish the two species. On the other hand, the size of the specimens at which the length approximates the height measure-

Table 3. Linear regression equations for the shell length and shell height of D-stage to recent postmetamorphic larvae. r^2 = coefficient of determination, P = probability for the slope of each regression, N = sample size. Slopes with different superscripts are significantly different ($P < 0.05$) by a Tukey multiple range test.

Species	Intercept	Slope	r^2	P	N	Author
Teredo navalis[1]	−49.03	1.40^{A}	0.99	<0.01	10	Fuller *et al.* (1989c)
Bankia setacea	−22.50	1.14^{B}	1.00	<0.01	8	Turner & Johnson (1971)
Bankia gouldi	−38.72	1.34^{A}	1.00	<0.01	6	Culliney (1975)
Bankia gouldi	−36.13	1.37^{A}	0.99	<0.01	7	Mann & Gallager (1985)
Bankia gouldi[1]	−32.56	1.28^{A}	0.98	<0.01	10	This study

[1] Data used to calculate the linear regression equations are derived measurements of the left valve of scanning electron micrographs. Analysis of covariance of the slopes is significant (F-statistic = 6.32, $P < 0.001$).

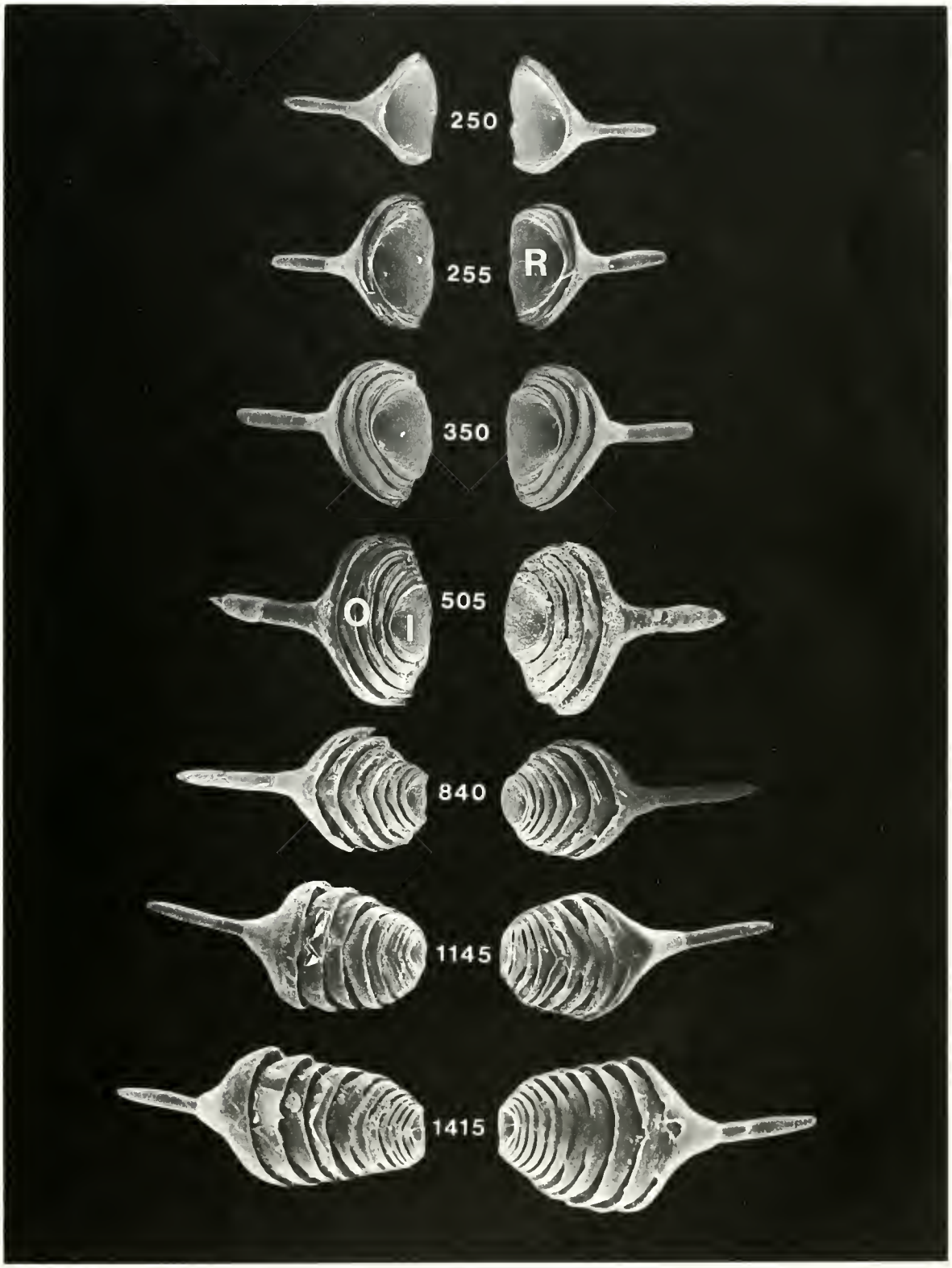

Figure 11. Outer surface view of the pallets. The pallet length is the distance between the proximal (stalk) and distal end (blade). Numbers signify the average length of the left and right (R) pallets. Dorsal side of the pallet is oriented towards the top. I = inner wall, O = outer margin of outer wall.

measurements can not be used to differentiate *B. gouldi* from *T. navalis*. The length and height of the larval shell of *B. gouldi* are nearly equal at about 143 μm, far beyond the point where the umbo is first visible in a shell in our standard orientation, at about 128 μm (Fig. 1). Culliney (1975) as well as Mann and Gallager (1985) reported that *B. gouldi* is equidimensional at 128 μm and 71.4 μm, respectively. This difference (144 μm vs 128 or 71.4 μm) is probably due to foreshortening (shells tilted) in the earlier studies. Fuller *et al.* (1989c) reported that *T. navalis* achieves equidimensionality at 150 μm. The initial size of a *B. gouldi* larva, is much smaller than that of the larviparus *T. navalis* due to differences in their development. Despite the difference in initial larval shell size, both species metamorphose at a shell height of about 230 μm, as indicated by the appearance of the ligament pit.

Table 3 shows that shell height increases faster than shell length until just before metamorphosis in *Bankia gouldi* (Culliney, 1975; Mann & Gallager, 1985), *Teredo navalis* (Fuller *et al.*, 1989c), and *Bankia setacea* (Tryon, 1863) (Turner & Johnson, 1971). The slopes are significantly different (P = <0.001) as shown by an analysis of covariance. Moreover, a Tukey multiple comparison test reveals that the slope for *B. setacea* is significantly lower than the other four species (P = <0.05, Table 3). The data for *B. gouldi* (this study) and *T. navalis* (Fuller *et al.*, 1989c) are from measurements of SEM micrographs of disarticulated left valves, whereas the data from other studies are based on light microscope measurements of articulated valves (Culliney, 1975; Turner & Johnson, 1971; Mann & Gallager, 1985). We have included the data from shells of recent postmetamorphic larvae since the ligament pit, an early indicator of metamorphosis, is difficult to detect by the previous studies.

The larvae of *Bankia gouldi* and *Teredo navalis* can be distinguished on the basis of the length of the provinculum on the left valve. The average length of the provinculum/hinge-line measured from micrographs of the left valves of *B. gouldi* (38.1 ± 1.8μ m, n = 9; Table 1) and *T. navalis* (46.7 ± 1.3 μm, n = 9; Fuller *et. al.*, 1989c) are significantly different (Student t-test, P < 0.001). Culliney (1975) reported a similar difference between the hinge-line length of *B. gouldi* (40.4 ± 3.96 μm, n = 35) and *T. navalis* (51.3 ± 2.19 μm, n = 47). The same conclusion is reached using a simple size of 21 for *B. gouldi*. The provincular length measurements of the left valve are more useful than those of the right valve, because the latter varies significantly with growth.

The larvae of *Bankia gouldi* and *B. martensi* (Stempell, 1899) can be distinguished from *Teredo navalis* by the length of the posterior provincular tooth of the left valve. The left posterior tooth of *B. gouldi* (6.4 ± 0.6 μm, n = 7) and *B. martensi* (6.4 ± 1.0 μm, n = 10) are significantly shorter that that of *T. navalis* (8.2 ± 0.3 μm, n = 9).

Close examination of the internal shell surface of the valves of *Teredo navalis* (see Fig. 1; Fuller *et al.*, 1989c) reveals a lateral hinge system similar to that in *Bankia gouldi*. The longer anterior component of the lateral hinge system in larvae of *B. gouldi* longer than 109 μm appears to be due to slightly faster growth of the anterior shell margin relative to the posterior shell margin. This difference may be useful in differentiating the two species.

Postlarval shell: Larvae of *Bankia gouldi* and *Teredo navalis* can be distinguished by the number of ridges vs. shell length in shells greater than 1 mm in length. Both species develop a denticulated ridge at about 0.24 mm in length. Denticulated ridges are added at about the same rate in both species until the shell reaches 1 mm. Subsequently, the number of denticulated ridges in *T. navalis* exceeds that in *B. gouldi*. For example, at a shell length of 2mm, *B. gouldi* has 13 ridges, compared to about 28 ridges in *T. navalis*. In the early larval stage of *B. gouldi*, the right valve is longer than the left valve (Fig. 8), but the degree of asymmetry is less than that in *T. navalis*. The shape of the later, postlarval shell varies greatly with the type of wood used as a substratum by the teredinids (Turner, 1966; Turner & Johnson, 1971), and the environmental conditions at the collection site (Hill & Kofoid, 1927).

Pallet: The morphology of the adult pallet is important in identification of teredinid species (Turner, 1966; 1971). In *Bankia setacea*, the pallet first appears at an early postlarval shell length of 0.5–0.6 mm (Quayle, 1959). In *B. gouldi*, the smallest individual with a pallet had an early postlarval shell length of 0.4 mm. The pallet at this early developmental stage is unsegmented and may be confused with the nonsegmented pallet of other teredinids. Caution is advised in using pallet morphology as a taxonomic tool at this developmental stage.

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A Simple Method for the *In Vitro* Culture of *Perkinsus marinus*

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INTRODUCTION

The oyster pathogen *Perkinsus marinus* Levine, 1978 is an apicomplexan protist that has caused substantial mortality among oyster populations along the mid-Atlantic and Gulf coasts of the United States and may be capable of cross-transmission among certain bivalve species (Goggin et al., 1989). The life cycle of the organism has been described previously (Mackin & Boswell, 1956; Perkins, 1966; Perkins & Menzel, 1966). Although many stages of the life cycle have been addressed, little evidence relative to mode of infection, infiltration and invasion has been described under *in vitro* conditions. Such information would provide insight into many hitherto unobservable aspects of the host/parasite relationship *in vivo*. This study demonstrates that certain vegetative reproductive aspects in the life cycle of the organism, normally occurring in the host, can be duplicated under relatively simple *in vitro* conditions.

MATERIALS AND METHODS

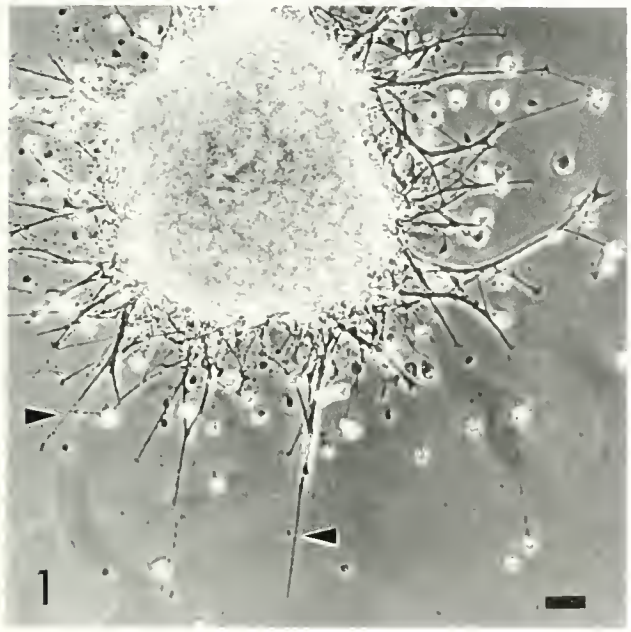
Parasitic cells were isolated from primary cultures of tissue explants of visceral ganglia of *Crassostrea virginica* Gmelin, 1791 and identified as *Perkinsus marinus* using the technique of Ray (1952). Following isolation of the protist, various mixtures of Leibowitz's (1952) medium (L-15), oyster hemolymph, fetal bovine serum (FBS), various sugars, yeast extract and lactalbumin hydrolysate were tested for cell growth potential. The osmolarity of each liquid component was adjusted to 750 mOs/kg by the addition of sea salts. The pH of each medium and/or constituent was adjusted to 7.6 and filter sterilized. Cultures were grown at 28°C in T-flasks under ambient CO_2/O_2. Penicillin G (100 U/ml) and streptomycin (0.1 mg/ml) were routinely added to all cultures and the medium (50%) exchanged weekly.

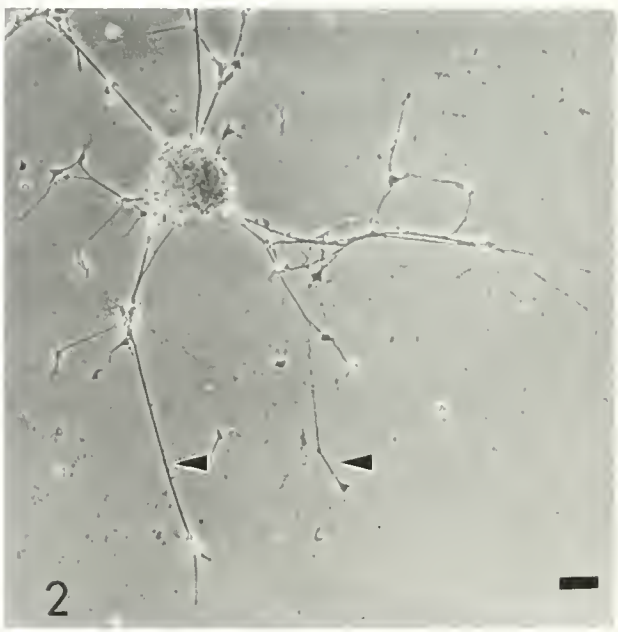
Mantle tissue for challenge experiments was from *Perkinsus*-free oysters which were routinely biopsed and maintained in isolated aquaria. Sterile explants were obtained by culturing the tissue for 4 days at 25°C in a 1:1 sterile sea water/hemolymph mixture supplemented with penicillin G (100 U/ml), streptomycin (0.1 mg/ml) and amphotericin B (0.25 μg/ml).

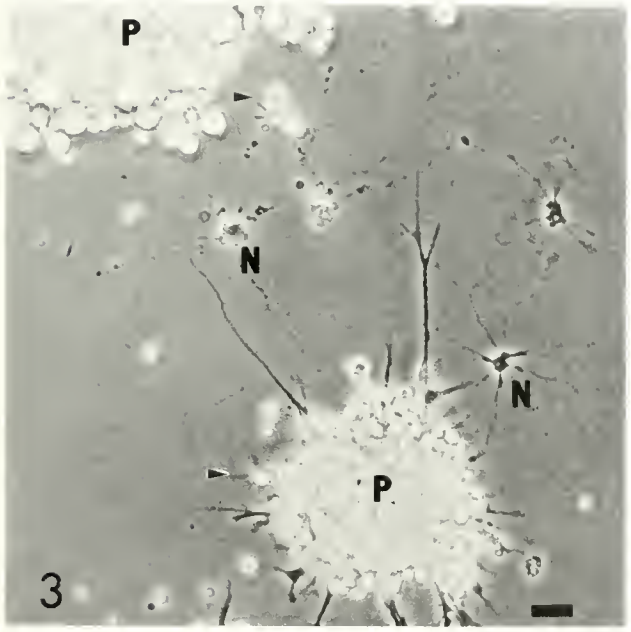
RESULTS

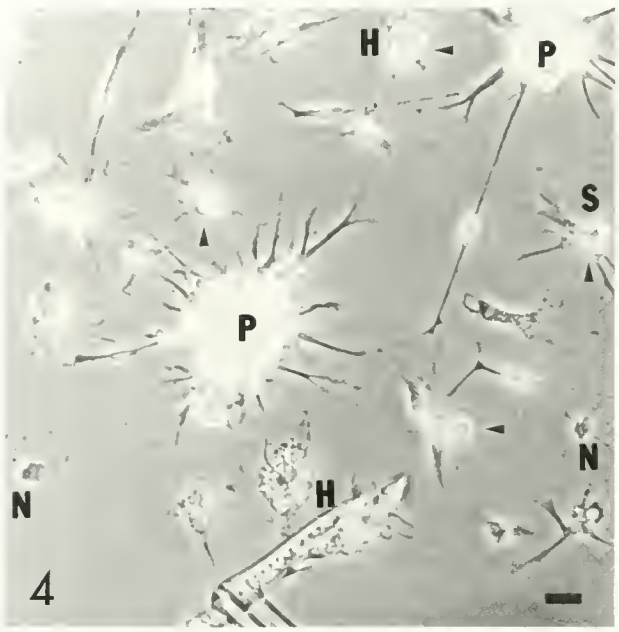
Healthy explant cultures of visceral ganglia of *Crassostrea virginica* are seen in figures 1 and 2. Similar explant cultures being parasitized by *Perkinsus marinus* are seen in figures 3 and 4. Colonization of large and small groups of oyster nervous tissue is readily apparent as is the attachment of parasitic cells to individual oyster cells. Various media preparations to be evaluated for optimal growth were inoculated with parasitic cells from similar cultures. Approximately two weeks after inoculation, it was evident that all media preparations evaluated would support cell growth to varying degrees. Cultures containing a high percentage of hemolymph displayed vigorous and rapid propagation (figures 5 and 6). Cells cultured with a high percentage of L-15 and/or FBS (50%) tended to differentiate into cells that resemble prezoosporangia (figure 5, double arrows) (i.e., large cells greater than ca. 20 um with the cellular volume consisting mostly of a vacuole and the cytoplasm occupying the perimeter of the cell; as described by Perkins and Menzel, 1966). Many non-flagellated daughter cells were formed in those cells yielding the morula-like cell aggregates typical of *Perkinsus marinus*. Upon rupture of the mother cell wall the daughter cells are released into the medium (figures 5 and 6, arrows). Shortly after release of the daughter cells, until enlargement to form prezoosporangium-like cells, they had the typical *Perkinsus marinus*-like meront structure consisting of a prominent, eccentric vacuole (figure 6, double arrows) with a single vacuoplast (figure 6, V arrow) and a single nucleus located near the cell wall.

The most successful medium preparation, yielding relatively large numbers of cells as well as a diversity of





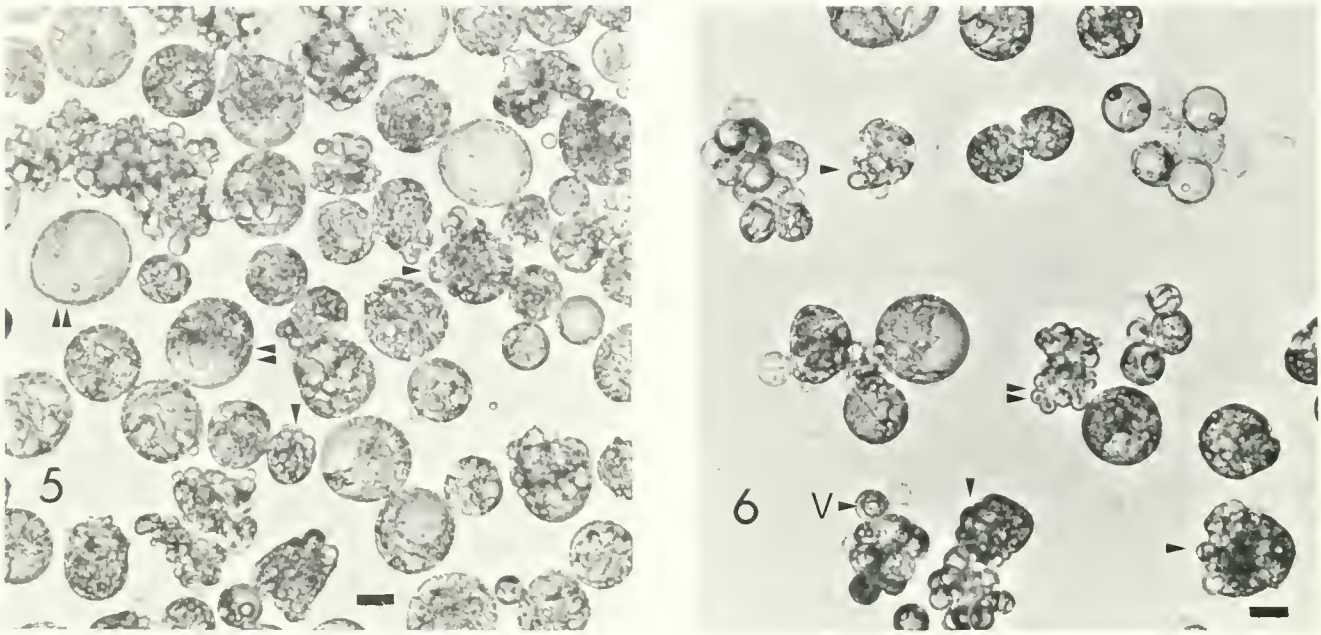




Figures 1–2. Photomicrographs of healthy visceral ganglion explants from *Crassostrea virginica*. Neurite growth extending from explants indicated by arrows, scale bar = 0.1 mm.

Figures 3–4. Photomicrographs of oyster ganglion explants parasitized by *Perkinsus marinus* (P). Notice individual neurons (N), support cells (S), hemocytes (H) and attachment of parasitic cells to individual oyster cells (arrows), scale bar = 0.05 mm.

life cycle stages consisted of a 100 ml. solution of L-15 containing 10.0 ml. of FBS, 20.0 ml. of oyster hemolymph, 5.0 mg. taurine, 50.0 mg. glucose, 30.0 mg. galactose, 50.0 mg. fructose, 50.0 mg trehalose, 100.0 mg. yeast extract, 300.0 mg. lactalbumin hydrolysate, 1.0 ml MEM vitamin solution (100X)(Sigma Chemical Co.) and 0.1 ml lipid mixture (1000X)(Sigma Chemical Co.). Cultures were routinely sub-cultured over a period of several months. Sterile mantle tissue was challenged with cultured *Perkinsus marinus* and became infected within 2-3 weeks. In fluid thioglycollate medium the parasite cells from challenged tissue formed cells resembling the prezoosporangia (or "hypnospores") normally seen in oyster tissue infected with *Perkinsus marinus*. The cells also stained like *Perkinsus marinus* prezoosporangia in Lugol's iodine solution (Ray, 1952).



Figures 5–6. Photomicrographs of groups of propagative cells of *Perkinsus marinus in vitro* Larger groups represent several generations. Figure 5. Notice presporangial cells (double arrows) and non-flagellated daughter cells (single arrows). Figure 6. *Perkinsus*-like cells with meront structure (double arrows), vacuoplast (V arrow) and non-flagellated daughter cells (single arrows), scale bar = 0.05 mm.

DISCUSSION

It is hoped that the technique described herein will contribute to the understanding of the basic biology of this parasite as well as to the host/parasite relationship. Refinement of culture conditions and further definition of nutritional requirements of the parasite *in vitro* would be particularly helpful as cellular or molecular approaches to this understanding are attempted.

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On the Identification of Fossil Terrestrial Gastropod Eggshells

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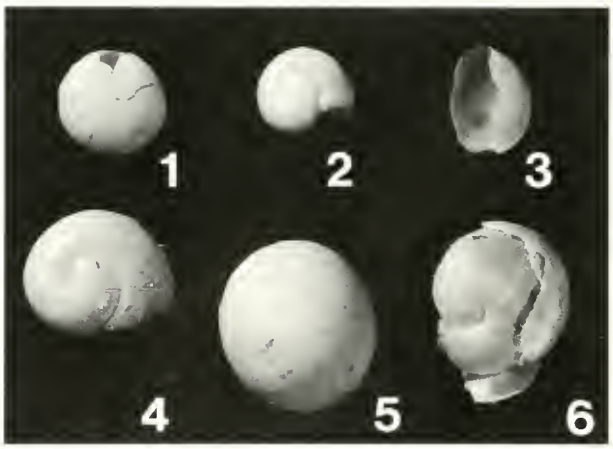
Small (~1 mm), calcareous spheroids, often oblate, are frequently recovered associated with nonmarine mollusks from Quaternary localities on the High Plains. In general, these eggshells of terrestrial gastropods have been ignored by modern paleontologists. Tompa (1976a) correctly correlated fossil eggshells from two middle Pleistocene localities in Kansas with the genus *Vallonia*. Tompa followed with a benchmark paper (Tompa, 1976b) in which he illustrated the eggshells of many taxa and provided a catalog of terrestrial species with partially or wholly calcified eggshells. Improved, and gentler, preparation techniques have resulted in encountering both a greater abundance and frequency of these gastropod eggshells, especially in material of mid-Pleistocene to Recent age. Recently, I recovered a substantial number of much older (21–28 Ma) gastropod eggshells from the Oligocene-Miocene Cabbage Patch fauna of southwestern Montana. Since these eggshells were associated with a prolific and diverse terrestrial gastropod fauna (Pierce, 1992), an attempt was made to identify the taxa that produced these eggshells.

In almost all cases, microscopic examination by transmitted light, and careful dissection of some specimens, has shown the fossil eggshells to be empty. Correlation of the eggshells with the various taxa in the fauna can be accomplished by comparison of hatchling size and shape to the size and shape of the eggshells. The two types of Cabbage Patch eggshells were both oblate spheroids that differed primarily in size (Table 1). The smaller eggshell matched very closely, in all dimensions, measurements of the hatchlings of *Vallonia berryi* Pierce, 1992, from the same fauna. The larger eggshell type was found to be marginally large enough, but too oblate, to accommodate hatchling of *Orcohelix brandi* Pierce, 1992, another component of this fauna. This match was also rejected on the basis that modern *Orcohelix* are oviparous. Hatchlings of another species, *Polygyroidea montivaga* Pierce, 1992, were a near perfect match, both in size and shape. No other taxa of this fauna had hatchlings that corresponded to the measurements of these eggshells (Pierce, 1992).

Current work involving the Skull Creek locality in Butler County, Nebraska (late Pleistocene: Wisconsinan: Peoria loess, ca. 20 Ka), provided a new collection of gastropod eggshells. The Skull Creek material contains at least two quite different eggshell forms (Table 1). The first, an oblate spheroid, H/W = 0.68, was very thin and delicate, and is represented by only 8 specimens, half of which are broken. In size and H/W, it compared closely with the eggshells attributed to Oligo-Miocene *Vallonia berryi*, and to mid-Pleistocene to Recent *Vallonia pulchella* (Müller, 1774) (Tompa, 1976a). Measurements of hatchling gastropods recovered as part of the Skull Creek locality fauna showed that hatchlings of *Vallonia gracilicosta* Reinhardt 1883, averaging 0.7 mm × 0.55 mm, were an excellent fit, in both size and shape, for this eggshell (Figures 1–3). The second eggshell type is a near spheroid, H/W = 0.93 or greater, and occurs in two slightly overlapping size ranges, each with distinct modes. The larger eggshell of this type is quite abundant (>50) (Figures 4–6). This eggshell size and shape was found to be an approximate fit for hatchlings of three taxa found in this fauna, all of which are known to have calcified



Figures 1–3. Small fossil eggshells and hatchling of *Vallonia gracilicosta* Reinhardt, 1883. **1.** Eggshell with crack and small fragment missing, lot PMSC 1002. **2.** Hatchling *V. gracilicosta*, lot PVAL 1002. **3.** Broken eggshell, lot PMSC 1002.

Figures 4–6. Large eggshell with embryo and hatchling of *Discus whitneyi* (Newcomb, 1864). **4.** Hatchling *D. whitneyi*, lot PDIS 1004. **5.** Large eggshell, lot PMSC 1001. **6.** Embryonic *D. whitneyi* still retaining portions of its eggshell, PDIS 1016. All figures 20×, all from Skull Creek locality, Butler County, Nebraska

Table 1. Measurements (in mm) of fossil gastropod eggshells.

Eggshells	N	Width/SD Range	Height/SD Range	H/W
Oligo-Miocene taxa				
Cabbage Patch molluscan fauna				
Vallonia berryi	10	0.76 ± 0.03 0.72–0.80	0.57 ± 0.02 0.55–0.60	0.75
Polygyroidea montivaga	10	1.60 ± 0.03 1.55–1.65	1.24 ± 0.04 1.15–1.30	0.78
Late Pleistocene taxa				
Skull Creek molluscan fauna				
Vallonia gracilicosta	4	0.80 ± 0.00 0.80–0.80	0.55 ± 0.00 0.55–0.55	0.68
Discus whitneyi	10	1.20 ± 0.03 1.15–1.25	1.13 ± 0.01 1.12–1.15	0.94
Discus whitneyi? small	5	1.03 ± 0.05 0.95–1.10	0.96 ± 0.04 0.90–1.00	0.93

eggshells (Tompa, 1976b, table 1): *Nesovitrea hammonis electrina* (Gould 1841), averaging 1.15 mm × 0.75 mm, *Zonitoides arboreus* (Say 1816), averaging 1.1 mm × 0.8 mm, and *Discus whitneyi* (Newcomb 1864), averaging 1.1 mm × 0.8 mm, with the latter two providing the best fit. [Roth (1987:129) has shown *D. whitneyi* to be a senior synonym of the well known *D. cronkhitei* (Newcomb, 1865)]. By chance, one eggshell contained a embryo, identifiable as *D. whitneyi* (Figure 6). Both *V. gracilicosta* and *D. whitneyi* are very abundant (>200 specimens each) components of the Skull Creek molluscan fauna. *Zonitoides arboreus* and *N. hammonis electrina* are less common (16–50 specimens each) components. A second, smaller set (N=5) of the nearly spheroidal eggshell type, microscopically indistinguishable from the larger size, could not be matched precisely with any other taxon, but would fit the extreme minimum hatchling size of both *D. whitneyi* and *N. hammonis electrina*. Tompa (1976b:867) has shown that, for some taxa, eggshell size varies from individual to individual, and/or with size of parent animal. It appears probable, therefore, that these also represent *D. whitneyi* eggshells, but from small parents.

Identification of eggshell types provides yet another tool useful in reconstructing fossil faunas. As more eggshells are identified to genus and/or species, it may become possible that additional taxa, represented only by eggshells in a fauna, can be identified, thereby increasing the recognized diversity of the fossil fauna and the accuracy of paleoenvironmental reconstruction. However, with rare exceptions requiring SEM examination (Tompa 1976b), identification beyond generic level is, at this time, often tenuous.

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Two New Tropical Western Atlantic Species of *Epitonium*, with Notes on Similar Global Species and Natural History

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ABSTRACT

Two large (up to 16.9 and 25.3 mm long), many-ribbed, shallow water species of *Epitonium* are newly described: *E. phymanthi* from southeast Florida, the Bahamas, and the West Indies, and *E. worsfoldi* from the Bahamas and the West Indies. Where possible, rib counts were made on each shell whorl to allow for ontogenetic changes. *Epitonium phymanthi* lives with and feeds on the sea anemone *Phymanthus crucifer* in Florida (where *E. lamellosum* and another epitoniid *Opalia crenata* also live with this anemone). Likewise, *E. worsfoldi* lives with and feeds on a sand-dwelling anemone that is either *Actinoporus elegans* or *Homostichanthus duerdeni* in the Bahamas. There it is more commonly parasitic on another anemone, *Stichodactyla helianthus*. Aquarium observations on *E. phymanthi* with *E. lamellosum* revealed some major biological differences between these co-occurring species, e.g. fully everted proboscis lengths and speed of movement. *Epitonium phymanthi* was found with *E. worsfoldi* at only one locality, as shells in the Virgin Islands.

Key words: Epitoniidae, new species, Western Atlantic.

INTRODUCTION

The family Epitoniidae contains a large number of described fossil and living species, and as with most groups of mollusks there is as yet no world monograph. In the interim, it could be argued that there should be a moratorium on describing any new epitoniids. The literature is very scattered and unsynthesized. There is not even a published list of names. Nevertheless, it is here believed that minimum requirements are met for describing two new species, albeit without anatomy.

This paper is a by-product of work on a book on the marine prosobranchs of the Bahamas being prepared by myself, Jack N. Worsfold, and Colin Redfern. New species are not being described therein.

The conchological systematics of Recent Epitoniidae (wentletraps) in the western Atlantic and eastern Pacific (where cognate forms, subspecies or species can be expected) are relatively well known thanks to Clench and Turner (1950b, 1951, 1952, 1953) and DuShane (1974, 1979). Little systematic work has since been done on the western Atlantic species. Even so, it was surprising to conclude that two large, many-ribbed, shallow-water *Epitonium* species had remained undescribed until now. One ranges from southeastern Florida and the Bahamas to the Lesser Antilles (Grenada). The other ranges from the Bahamas to Cuba, Puerto Rico and the Virgin Islands. Both may well have more extended ranges. As recently as 1967, one of the species was first collected alive; it was in less than 1 m of water within sight of a major marine laboratory!

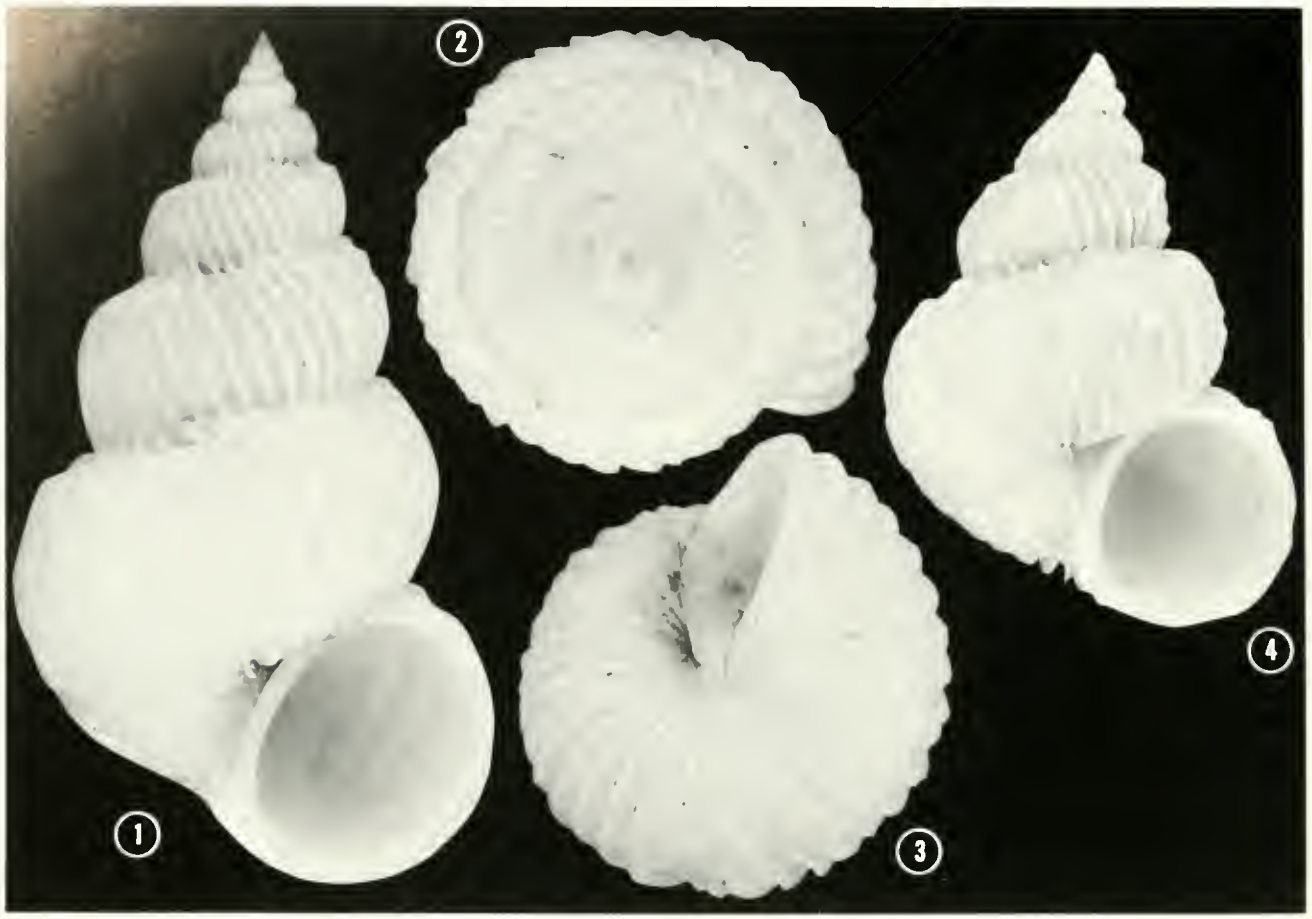
Clench and Turner had neither of these species available in the collections they studied [although a small, badly broken shell of one of them was mixed in a vial with one *E. albidum* (Orbigny, 1842) (MCZ 107820).

Some epitoniid species seem possibly or probably to be circumglobal (Robertson and Habe, 1965; Kilburn, 1972, 1985; DuShane, 1983; Paschall, 1987). Therefore, an attempt has been made to consider the two new species in a global context. Based on epitoniid collections at MCZ, AMNH, ANSP and USNM and literature, shells of 23 species from around the world (Appendix) were assessed to be most similar to the shells described here.

I have tried to survey all the descriptions and illustrations of Miocene to Recent species of *Epitonium*, *sensu lato*, known from the Americas, and of most Recent species from here and the rest of the world, especially Europe and the Mediterranean. These are the fossils and living animals most likely to be similar or identical to the shells discussed here. European fossil epitoniids were not surveyed because the literature is so extensive. Among the most important references consulted on *Epitonium*, *sensu lato* are:

1) world Recent species: Kiener (1838–1839); Sowerby (1844); Nyst (1871); Sowerby *in* Reeve (1873–1874); Tryon (1887); Clessin (1896–1897); de Boury (1912–1913); Kaicher (1980, 1981, 1983, the only really global contribution in this century, albeit incomplete).

2) American Recent species: Mörch (1875a, 1875b, 1876); Dall (1889); Clench and Turner (1950a–1953); Nowell-



Figures 1–4. *Epitonium phymanthi* Robertson, new species. **1.** Apertural, **2.** apical, and **3.** basal views of holotype. Shell 16.9 mm long, and 9.3 mm wide. Miami, Florida ANSP 391939. **4.** Unusually low-spired shell (not a paratype), 12.0 mm long, and 8.6 mm wide.

Usticke (1959); Keen (1971); Abbott (1974); DuShane (1974, 1979, and references therein); Gundaker (1975); de Jong and Coomans (1988); Espinosa and Fernandez Garcés (1990).

3) American late Cenozoic fossil species: Olsson (1916); Maury (1910, 1917); Gardner and Aldrich (1919); Pilsbry (1922); Woodring (1928, 1959); Mansfield (1930, 1935); Pilsbry and Olsson (1941); Gardner (1947, 1948); Olsson and Harbison (1953); Weisbord (1962); Jung (1969).

4) European Recent species: Parenzan (1970); Franchini (1975–1976); Nordsieck (1982); Bouchet and Warén (1986); Poppe and Goto (1971).

5) Indo-Pacific, Japanese, Australasian and South African Recent species: Adams (1861); Melvill and Standen (1903); Jousseaume (1911); Iredale (1936); Kerslake (1958); Azuma (1962); Macpherson and Gabriel (1962); Kuroda, Habe and Oyama (1971); Masahito and Habe (1973–1976); Powell (1979); Kilburn (1985); DuShane (1988, 1990); Nakayama (1991).

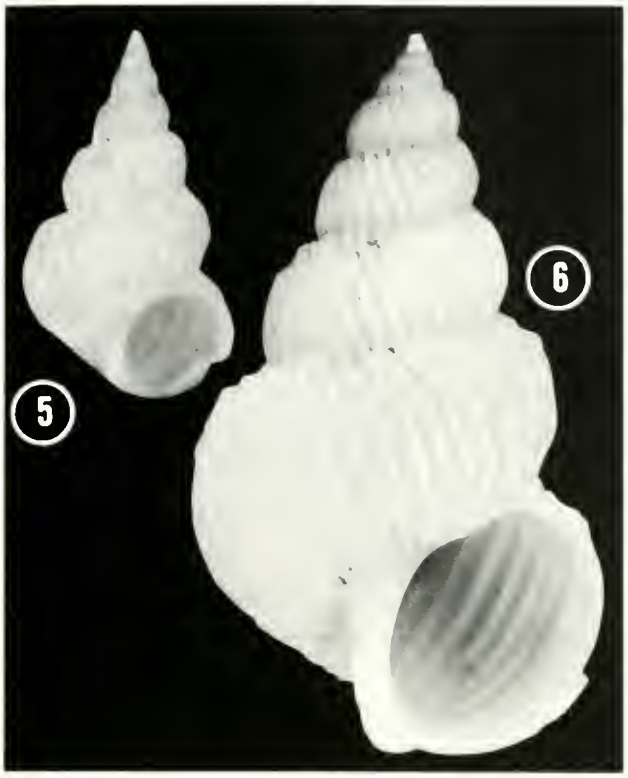
An attempt was made to count the ribs on each whorl of each shell. The need for doing so was explained in a previous paper (Robertson, 1983a). Counts on juveniles can be different from those on adults. Indeed, a rib count per whorl in species of *Epitonium* may increase, stay the same, decrease, or decrease and then increase as the shell grows in a species-specific manner. These taxonomic characters have hardly been used before.

The major study by Clench and Turner (1950b–1953) was published before epitoniids were found to live with or to forage for and feed on benthic coelenterates, either as parasites or predators (Thorson, 1957; Robertson, 1963, 1981, 1983b; DuShane, 1988; Yamashiro, 1990; Nakayama, 1991, etc.). Both species treated here have actinian (sea anemone) hosts.

MATERIALS AND METHODS

The specimens studied were assembled during almost two and a half decades. The two shallow-water species are curiously uncommon, and I personally saw neither of them alive. Only empty shells are available of *E. phymanthi*, but there are a few *E. worsfoldi* in alcohol (see ANSP "A" numbers in locality records).

Shells were studied with the aid of a Wild dissecting



Figures 5–6. *Epitonium phymanthi*. Incompletely grown paratype shells. **5.** Only shell known from Bahamas, juvenile, 5.6 mm long, 3.1 mm wide. **6.** Subadult topotype, 10.8 mm long, 6.3 mm wide.

microscope and camera lucida. First-whorl diameters were measured and whorls counted as advocated by Robertson (1985). The camera lucida and a protractor were used to measure spire angles to the nearest 5°. Specimen numbers in the Specimens Examined sections relate to Tables 1 and 2.

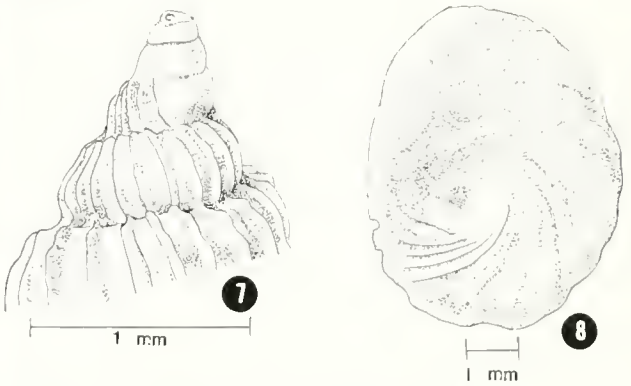
Rib counts were made on decollated shells by measuring the mean width of each whorl on intact shells and then extrapolating. As landmarks, some ribs were lightly marked with a pencil.

Repositories of examined specimens are indicated by the following acronyms:

AMNH—American Museum of Natural History, New York City
ANSP—The Academy of Natural Sciences of Philadelphia
MCZ—Museum of Comparative Zoology, Harvard University
USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS AND NATURAL HISTORY

Superfamily Epitonioidea
Family Epitoniidae
Genus *Epitonium* Röding, 1798



Figures 7–8. *Epitonium phymanthi* **7.** Shell apex, showing a slightly decollated protoconch apex, the almost smooth protoconch, the protoconch varix (shown as a line), some of the early teleoconch axial ribs, and fine intervening spiral threads. Topotype. **8.** Operculum (exterior). Topotype.

Epitonium phymanthi Robertson, new species
(figures 1–11, 13)

?*Epitonium* spec.: de Jong & Coomans, 1988:54, fig. 276 Curaçao.

Shell morphology: Protoconch 0.42–0.50 mm long (excluding immersed base), 0.39–0.42 mm wide, with 3.2–3.4 whorls; first whorl diameter 0.09–0.13 mm; whorls slightly inflated, appearing smooth, shiny, microsculpture probably present; terminated with varix; cream-white, tinged with amber at suture, terminal varix, and columella (seen in transparency); some protoconchs slightly tilted on teleoconchs. Entire shell reaching 16.9

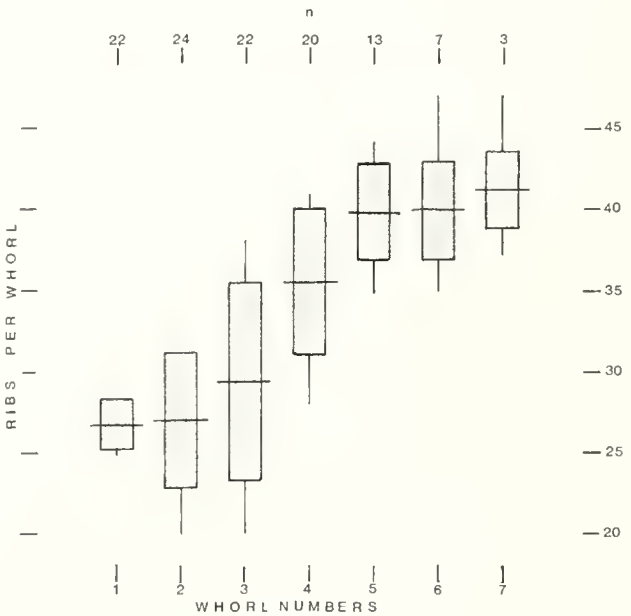


Figure 9. *Epitonium phymanthi* Rib frequencies per whorl on each whorl. The horizontal lines show means, the vertical stippled boxes show ± one standard deviation, and the vertical lines show ranges; n = sample sizes.

Table 1. *Epitonium phymanthi* new species. Mensural and meristic shell characters. "+" indicates that a shell would have been larger had it not been slightly broken, or "++" badly broken. Specimen 21 is the holotype. All remaining specimens are paratypes except specimen 28, which was not included in figure 9 because of the high rib counts.

Specimen no.	Length (mm)	Width (mm)	Spire angle	Teleoconch whorls	Axial ribs per whorl						
					1	2	3	4	5	6	7
1	2.2+	1.5+	60°	2.5+	25	29	—	—	—	—	—
2	3.1+	2.0+	55°	3.4+	23	24	—	—	—	—	—
3	3.0+	1.6+	45°	3.2+	21	23	22	—	—	—	—
4	2.3	1.5+	55°	2.8	27	26	—	—	—	—	—
5	3.5	2.2	50°	3.8	23	24	28	—	—	—	—
6	4.2+	2.7+	50°	4.3+	25	24	23	25	—	—	—
7	4.8	3.1	55°	4.4	28	29	29	29	—	—	—
8	5.5+	3.7+	60°	4.7	27	30	29	33	—	—	—
9	5.3+	3.3	55°	4.8	25	28	30	35	—	—	—
10	7.8	4.7	50°	5.6	27	29	28	36	45	—	—
11	7.8	4.6	50°	5.7	24	25	27	28	39	—	—
12	6.7	4.0+	50°	5.3	24	30	27	31	38	—	—
13	5.0+	2.3+	55°	3.7+	24	27	26	—	—	—	—
14	8.7+	4.4+	55°	5.3+	24	—	28	37	44	—	—
15	12.2+	3.9+	50°	5.2+	—	26	25	29	—	—	—
16	8.6+	5.2+	50°	5.8+	—	23	26	36	42	—	—
17	9.5+	5.2+	50°	6.3+	24	24	21	26	32	42	—
18	11.2+	6.7+	50°	6.4+	27	28	29	30	35	45	—
19	10.3+	5.8+	45°	6.2	22	24	24	26	31	39	—
20	11.4	8.1	60°	6.2	23	21	23	26	33	34	—
21	16.9	9.3	55°	7.2	21	22	21	24	33	35	38
22	16.6	9.6	65°	7.7	23	24	22	23	26	34	40
23	15.3+	8.8	55°	6.2	—	21	25	26	40	36	—
24	5.6	3.1	45°	5.1	22	25	24	24	27	—	—
25	9.1+	5.6	50°	5.7+	—	21	25	28	—	—	—
26	16.9	9.5	50°	7.8	18	18	27	30	39	37	37
27	6.0++	4.5	—	2.6++	—	—	—	34	—	—	—
28	8.6++	4.6++	—	2.8++	—	—	39	45	—	—	—
29	5.9++	4.1++	—	1.6++	—	—	—	—	—	—	—

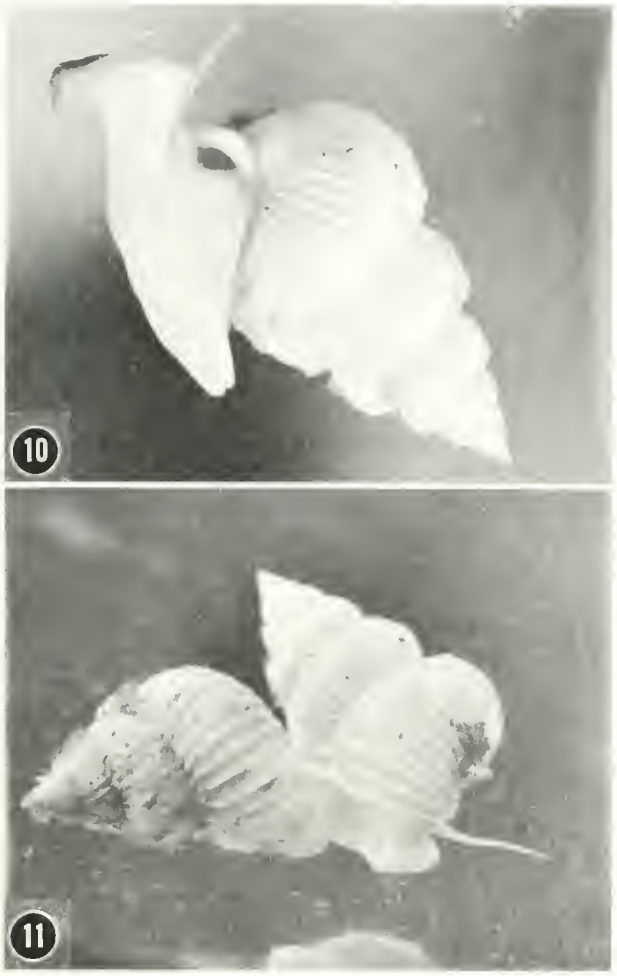
mm (Table 1). Teleoconch to 9.6 mm wide (including ribs), with 7.8 whorls, initially thick, becoming relatively thin, fragile with increasing shell size. Spire height variable, usually low, spire angle 45°–65° (mean 53°; Table 1). Spire profile at first straight, convex on later whorls of large shells. Whorls moderately to strongly inflated. Axial ribs 18–45 per whorl, number increasing with shell size (figure 9; table 1); ribs thick, low, with edges rounded on upper whorls, thinner, higher, wavy or crested at shoulder on later whorls. Apical whorls fully attached to preceding whorls, lower whorls slightly detached. Axial ribs aligned, attached erectly from one whorl to the next on upper whorls, rib alignment and attachment decreasing with increasing shell size; ribs on later whorls rarely in closely spaced pairs or bifurcating; ribs commonly curled away from aperture. Fine, regularly spaced spiral threads between ribs on early whorls (about 12 above suture), later whorls with irregular threads, smooth or with fine incised spiral lines. Basal spiral cord lacking. Umbilicus narrow, or reduced to chink. Aperture obliquely to roundly oval. Teleoconch color cream-white or pure white. Operculum not available.

Comparative remarks: This new species differs from *E. worsfoldi* Robertson (see below) in that the latter species has a thicker more highly spired shell, with coarser, uncrested, less numerous ribs (especially on the last whorl of large shells). *Epitonium phymanthi* most closely resembles species assigned to de Boury's (1912) "subgenus" *Foliaceiscala* (Appendix). The most closely similar species seem to be *E. irregulare* (Sowerby, 1844) from the Philippines and Japan, and *E. virgo* (Masahito and Habe, 1976) from Japan (Appendix).

Etymology: Of *Phymanthus*, the genus of sea anemone host.

Geographic range: SE Florida, the Bahamas, Virgin Islands and Grenada (Lesser Antilles). Not known from Bermuda or the Greater Antilles.

Material examined: (Table 1): SE Florida: Bear Cut, Miami (25°43'N, 80°09' W), 1 m, N. and E. Leeman leg., 1965, Holotype—ANSP 391939, ANSP 391940 & ANSP 391941, specimens 19–23, Leeman collection 1 specimen. Bahamas: Dead Man's Reef beach, western Grand Bahama (26°34'45"N, 78°51'45"W), S. Bowers leg., Feb. 1981, via J.N. Worsfold, ANSP 374362, specimen 24. Virgin Islands: Lindbergh Bay, St. Thomas (18°20'N, 64°58'W), 2 m, M.R. Hyett leg., Oct. 30, 1968, ANSP,



Figures 10–11. *Epitonium phymanthi* living in aquarium. Topotypes.

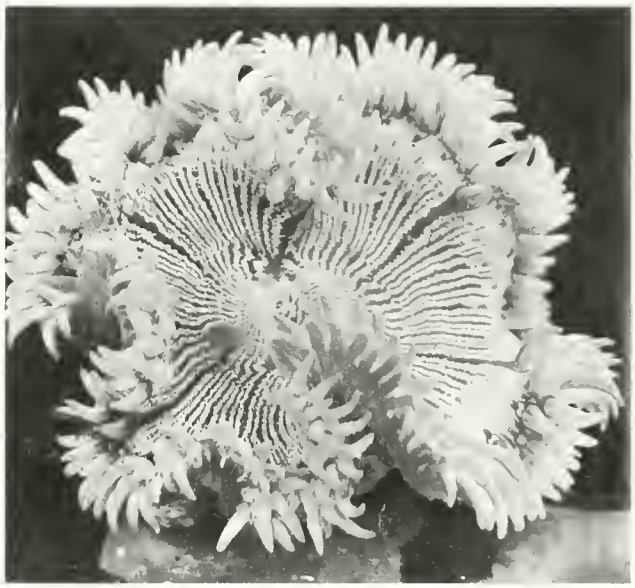


Figure 12. *Phymanthus crucifer*, the sea anemone host of *Epitonium phymanthi* at Miami, Florida. Size not recorded, but somewhat less than life size. The anemone colors and patterns vary considerably. Photo Neal Leeman.

specimen 26. Hams Bay, St. Croix (17°47′N, 64°53′W), G. Nowell-Usticke leg., Feb.-March 1957, AMNH 194365 (Specimens 1–18, 27–29)[co-occurred with 1 *E. worsfoldi*]. Lesser Antilles: Saint George's Lagoon, Grenada (12°03′N, 61°45′W), G. Nowell-Usticke Colln., AMNH 194429, Specimen 25. Specimen 21 is the holotype. All remaining specimens except unnumbered specimen in the Leeman collection and specimen 28 are paratypes.

A total of 29 specimens of *E. phymanthi* was available for this study. As with *E. worsfoldi*, many of the shells are broken.

Natural history: In 1965, Neal and Eleanor Leeman collected six living animals of *E. phymanthi* slightly below low tide line at a rocky area in Bear Cut, between Virginia Key and Key Biscayne, Miami, Florida, U.S.A. All were associated with the actiniarian sea anemone *Phymanthus crucifer* (Lesueur, 1817). The anemones were clinging to rock substrata, commonly in crevices, and turtle grass (*Thalassia testudinum* Banks and Solander ex König) rhizomes, most of which were buried in sand. The epitoniums were buried next to the *Phymanthus* columns under their radially extended oral discs. Only anemones buried in sand had *E. phymanthi* with them. A few clusters of sand-agglutinated *Epitonium* egg capsules were observed but not studied.

On April 17, 1965, a pair of *E. phymanthi* was found with one *Phymanthus*. On May 12, May 30, June 6, and August 8 of the same year, single *E. phymanthi* were found with *Phymanthus*. Unlike a predatory *Epitonium*, which swallows its coelenterate prey whole, *E. phymanthi* is a parasite, feeding on its large host polyp without killing it. When fully extended, a large specimen of *Phy-*

Figure 13. *Epitonium phymanthi* feeding on the upper column of its slightly contracted sea anemone host *Phymanthus crucifer*. Note the extraordinarily long everted acrembolic proboscis. Miami, Florida. Epitoniums, unlike pyramidellids, take tissues for food rather than fluids. Drawing based on photographs by Neal Leeman.

Figures 14–16. *Epitonium worsfoldi* Robertson, new species. **14.** Apertural, **15.** basal, and **16.** apical (at lower magnification) views of the holotype, 18.7 mm long, 9.1 mm wide. Smith's Point, Grand Bahama Island. ANSP A17192.

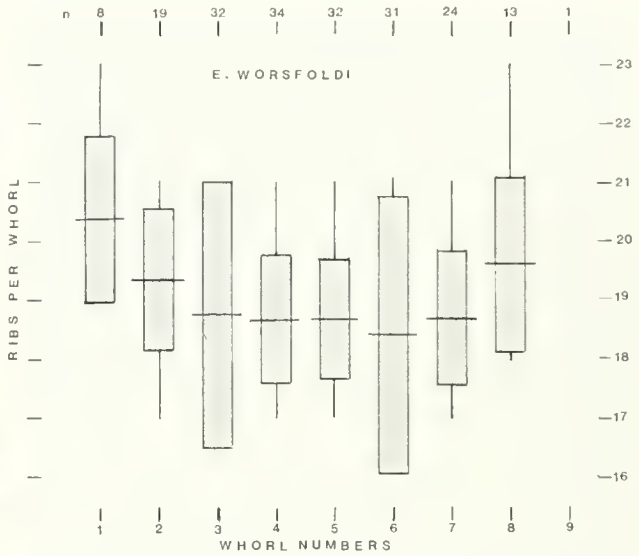


Figure 17. *Epitonium worsfoldi*, new species. Rib frequencies per whorl on each whorl. The horizontal lines show means, the vertical stippled boxes show ± one standard deviation and the vertical lines show ranges; n = sample sizes.

manthus crucifer is about 13 cm high and about 13 cm wide, much larger than the wentletrap.

Epitoniums can vary their host preferences from place to place. During the same year and months, at the same locality, and associated with the same species of sea anemone, the Leemans collected six living *Epitonium lamellosum* (Lamarck, 1822)(ANSP 391948, A16850) and one living *Opalia crenata* (Linnaeus, 1758)(ANSP A16851). Thus *Phymanthus crucifer* supports three parasitie epitoniid species at one locality. *E. phymanthi* may or may not be specific to *Phymanthus* elsewhere.

Colors and color patterns of *P. crucifer* vary considerably. Usually, these anemones are variegated with shades of green or brown. The white shell and body of *E. phymanthi*, and the white and reddish brown shell and nearly white body of *E. lamellosum*, make neither species cryptically colored with its host. At least during the day, both species are buried in sand next to the anemone.

The Leemans maintained *E. phymanthi* and *E. lamellosum* with *Phymanthus crucifer* in home aquaria from mid-April to mid-October, 1965 (two *E. lamellosum* for as long as three months). Their observations are abstracted below.

The external body coloration of *E. phymanthi* was white, that of *E. lamellosum* was white except for light yellowish tentacles that faded to white in aquaria. The fully everted proboscis of *E. phymanthi* was at least four times the shell length, while the fully extended proboscis of *E. lamellosum* was only slightly longer than the shell. Both species behaved as if they locate their host by chemotropism, using their tentacles and slightly everted proboscises as do two Californian species (Smith, 1977; Salo, 1977).

Both *E. phymanthi* and *E. lamellosum* were seen to feed on *Phymanthus* columns near the base and under the oral disc, ingesting column tissues (with fluid? mucus?). Anemone tentacles were not observed to be attacked by either species. Duration of feeding in *E. phymanthi* was 2–10 minutes (animals not starved; mean of 5 observations ca. 4 min.). *Epitonium lamellosum* (a larger species, up to 45 mm shell length) starved for 3–5 days fed for 45–97 minutes (mean of 4 observations: 64 min.). No purple secretion was seen to be released from the pigmented mantle organ by either species during feeding. One *Phymanthus* survived repeated attacks by the two species for upwards of one month. The anemone writhed near where it was attacked, and the column also swelled. The anemone reacted least to *E. phymanthi*, the smaller, slower species.

An *E. phymanthi* with a shell 7 mm long on August 11 grew to 11 mm by September 22, a mean rate of 0.11 mm/day. Growth initially was faster (between August 11 and 21: 0.2 mm/day), but there was no growth between September 22 and October 5. Another *E. phymanthi* fed and survived from August 11 to September 2 without growing (22 days). Growth of *E. lamellosum* was rather faster and also erratic, but growth appeared to be indeterminate (Leeman and Robertson unpublished).

Epitonium phymanthi was observed to move very slowly and remain motionless for long periods of time. *Epitonium lamellosum* was more active. On several occasions, *E. phymanthi* was observed following *E. lamellosum* mucous trails, and partially everting and inverting its proboscis, each time ending by touching an

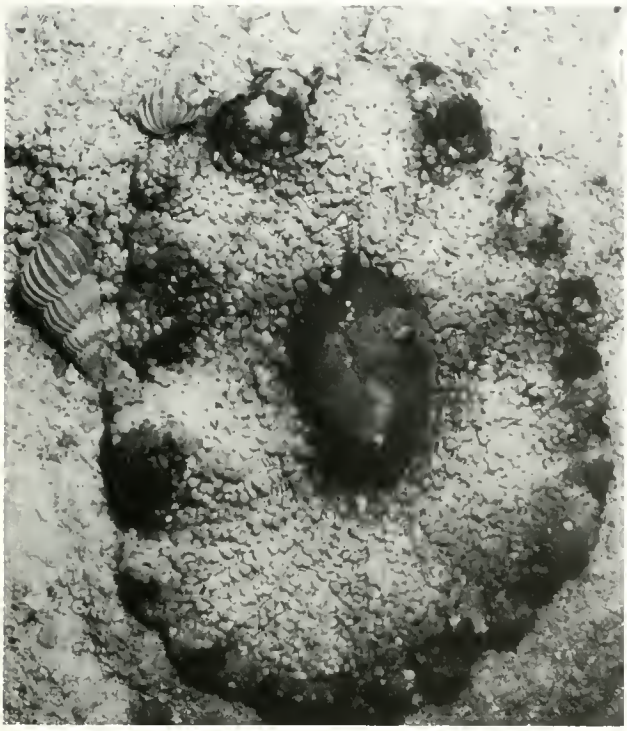


Figure 18. Oral view of either *Actinoporus elegans* or *Homostichanthus duerdeni*, a sand-dwelling sea anemone, showing beside it the holotype and egg capsules of *Epitonium worsfoldi* found with it. A paratype shell also shows. The anemone is 7.5 cm in greatest diameter. Smith's Point, Grand Bahama, Bahamas. Photo Jack N. Worsfold.

Figure 19. Living *Epitonium worsfoldi* near some of its sand-agglutinated egg capsules. Some of the shell ribs are abnormally bent. ANSP A17194. Shell 18.8 mm long, 9.8 mm wide. Grand Bahama. Photo Jack N. Worsfold.

E. lamellosum. On one occasion, an *E. lamellosum* approached an *E. phymanthi* in the same way. Once, individuals of the two species remained aperture to aperture for about one hour, with the four tentacles curled around each other.

Groups of egg capsules with *E. phymanthi* were found in early May, early June, and early October. After 36 days in isolation, one *E. phymanthi* had two groups of fresh egg capsules attached to it, indicating a capacity for sperm storage.

A small crab killed an *E. phymanthi* with a shell 10 mm long. Three other, larger animals died from unknown causes.

Epitonium worsfoldi Robertson, new species
(figures 14–19)

?*Turbo principalis* Pallas, 1774: 33, pl. 3, figs. 5–6. No locality. *Nomen dubium*. This species might not be large if the figures are enlarged. The spire angle (if accurately drawn) is 30°–35°.

?"*Scala principalis* (Pallas)": Mörch, 1875a, 1875b, 1876. Tortola, British Virgin Islands. Probably not of Pallas.

Unidentified. Huber, 1982: 202, 2 figs. S of Balmoral Island, Nassau, Bahamas. Reported to be 1 5/8" long (= 41 mm).

"*Epitonium principalis* (Pallas, 1774)": Paschall, 1986:66, figs. 1a and b. Next to a sea anemone, Green Turtle "Key" [Cay], Abaco, Bahamas. Not of Pallas. Reported to be 1.75 inches long (= 44 mm).

?*E. principale* "Röding, 1798": de Jong & Coomans, 1988:54, fig. 275. "Rather common in Curaçao and Aruba." Too few axial ribs.

?"*E. frielei* (Dall): Espinosa and Fernandez Garcés (1990:6), probably not of Dall; three small shells from Bahía Cienfuegos, Cuba, the longest 3.8 mm.

Shell morphology: Protoconch 0.52–0.54 mm long (excluding immersed base), 0.40–0.43 mm wide, with 4.1–4.2 whorls; first whorl diameter 0.12 mm; whorls slightly inflated; microsculpture as in *E. albidum* (Robertson, 1983b); white, with pale brown at suture, terminal varix. Entire shell attaining 25.3 mm (Table 2). Teleoconch to 11.5 mm wide (including ribs), with ca. 8.8 thin, fragile whorls. Spire high, spire angle 35°–50° (mean 44°); spire profile convex, rarely straight or initially concave; whorls moderately inflated. Axial ribs thick, low on upper whorls, thinner, higher, upright or recurved without subsutural or shoulder cresting (except remnants from breakage) on later whorls; numbering 16–21 on all but first and last whorls large shells (23 ribs on last whorl of 8.8+ whorl shell), with ribs/ whorl initially decreasing then increasing with shell size (figure 17); axial ribs on successive whorls usually attached, attachments erect, rarely offset away from aperture on lower whorls; rarely, all ribs bent medially after an injury (figure 19). Suture present in

Table 2. *Epitonium worsfoldi* new species. Mensural and meristic shell characters. "+" indicates that a shell would have been larger had it not been slightly broken, or "++" badly broken. Specimen 37 is the holotype.

Specimen no.	Length (mm)	Width (mm)	Spire angle	Teleoconch whorls	Axial ribs per whorl							
					1	2	3	4	5	6	7	8
1	17.9+	8.9+	45°	7.3+	—	—	21	18	18	18	18	—
2	18.8	9.8	45°	8.0	20	20	19	18	18	19	19	20
3	9.4	5.3	40°	6.5	20	20	20	19	19	20	—	—
4	8.8	5.4	45°	6.6	22	21	20	20	21	21	—	—
5	—	4.7	—	—	19	19	19	18	19	20	—	—
6	—	—	—	3.3	23	21	21	20	—	—	—	—
7	—	—	—	—	20	18	17	18	17	18	—	—
8	—	11.3+	—	ca. 8.8	—	—	—	—	—	—	—	20
9	22.1	10.3	40°	8.3	20	20	19	19	18	18	18	18
10	15.6+	7.7	35°	7.2	—	19	19	20	19	17	17	—
11	12.5	5.9+	40°	6.8+	19	19	19	18	19	20	—	—
12	17.2	8.0	40°	7.6+	—	—	21	20	19	19	19	—
13	14.3	7.2	40°	7.1	—	—	20	19	19	19	19	—
14	19.7+	9.9	40°	8.2	—	—	19	19	19	19	19	20
15	19.6+	9.7	40°	8.0	—	21	20	20	20	20	21	19
16	19.7	9.6	40°	7.8	—	20	18	17	18	18	18	—
17	14.9	8.1	40°	7.3	—	20	19	18	18	18	19	—
18	18.3	9.5	45°	7.9	—	17	18	18	17	18	18	—
19	19.2	9.2	40°	8.1+	—	—	21	19	19	19	19	23
20	4.4	2.4	40°	—	—	—	—	—	—	—	—	—
21	6.9	3.8	40°	5.4	—	20	18	19	19	—	—	—
22	25.3	11.5	45°	8.1	—	19	19	19	19	20	20	21
23	15.6	8.2	45°	8.0	—	—	—	—	—	—	—	—
24	21.5+	9.0+	40°	7.9	—	—	19	17	17	17	17	—
25	18.9+	9.2+	40°	7.8	—	—	—	19	19	19	—	—
26	17.7+	9.3+	45°	7.8	—	—	20	21	20	20	21	—
27	13.9+	6.4+	40°	6.9+	—	—	18	18	18	—	—	—
28	19.4	9.6	45°	7.7	—	—	20	20	20	20	20	—
29	15.0+	7.5+	45°	7.1	—	20	18	18	17	17	17	—
30	18.6+	10.0	40°	7.2	—	—	—	18	18	18	19	19
31	20.2	10.7	45°	8.2	—	18	18	18	18	18	18	19
32	18.8+	10.0	45°	8.0	—	—	18	18	18	18	18	19
33	22.4+	—	45°	8.3	—	—	20	20	20	20	19	21
34	17.1	8.4	45°	7.7+	—	—	18	17	18	18	18	19
35	12.9	7.2	45°	7.1	—	17	17	18	—	18	18	18
36	10.2+	4.7+	50°	5.5+	—	—	17	17	19	18	—	—
37	18.7	9.1	45°	7.8	—	19	19	20	20	19	20	—
38	6.0++	2.9++	45°	5.6++	—	—	—	—	—	—	—	—

inter-rib areas of uppermost whorls; middle, lower whorls slightly detached. Areas between axial ribs with faint, irregularly-spaced, incised spiral lines; axial growth lines present. Body whorl without basal spiral cord. Umbilical chink narrow (rarely almost closed). Columellar callus thin or thick, thinnest medially, not conforming to underlying ribs. Columellar chinks present. Aperture roundly oval. Teleoconch color pale tan, cream-white, pure white (when bleached?). Operculum paucispiral, growth wrinkles present, pale amber.

Comparative remarks: *Epitonium worsfoldi* most closely resembles species in the de Boury "subgenera" *Hyaloscala* [1889], *Limiscala* [1909], and *Papyriscala* [1909] (see Appendix) as discussed in Kilburn (1985). The shell of *E. worsfoldi* most closely resembles *E. kraussi* (Nyst, 1871) of South Africa and *E. melior* (Melvill and Standen, 1903) of the northern Arabian Sea (see Appendix).

Etymology: Named for Jack Nigel Worsfold, indefatigable naturalist and friend.

Geographic range: Bahamas, northern Cuba, and Puerto Rico. Not known from Bermuda, Florida, or the Lesser Antilles.

Material examined: (Table 2): Bahamas: Fleming Road beach, Mosquito Point, 8 km SE of West End, Grand Bahama (26°37′30″N, 78°54′00″W), J.N. Worsfold leg., ca. 1976, ANSP 370051, specimen 33.- Smith's Point, Grand Bahama (26°31′N, 78°37′W), 1 m, 1 living under *Stichodactyla* ["*Stoichactis*"] *helianthus*, 1 large, with egg capsules, living under either an *Actinoporus elegans*

or *Homostichanthus duerdeni* (Figure 18), J.N. Worsfold leg., August 1985, ANSP A17192, Holotype, ANSP A17193, specimens 35, 37.—SW of Sharp Rocks Point, near Peterson's Cay, S coast central Grand Bahama (26°33′45″N, 78°33′30″W), 1 m, 2 juveniles living with egg capsules under *Stichodactyla*, J.N. Worsfold leg., June 1984, ANSP A17194.—Gold Rock, S. coast central Grand Bahama (26°36′15″N, 78°22′15″W), 1 m, 2 juveniles living under *Stichodactyla*, J.N. Worsfold, leg., June 1984, ANSP A17195.—Treasure Cay and vicinity, Abaco, 12 shells, C. Redfern leg., Redfern collection, specimens 7, 23–32.—W coast N end Elbow (Little Guana) Cay, off NE Abaco (26°33′00″N, 76°56′45″W) K. A. Robertson leg. ca. 1954, ANSP 359100, specimen 16.—Wood Cay, Schooner Cays, W of S Eleuthera, M. McNeilus leg., Dec. 1980, McNeilus collection, specimen 1.—North East Point, Arthurstown, Cat Island (24°38′N, 75°38′W), 1 broken shell with an *E. albidum*, W.J. Clench and H.D. Russell leg., 1936, MCZ 107820, specimen 36.—Bahamas unlocalized, ANSP uncatalogued, specimen 34. Cuba: NW coast, Oasis Beach, Via Blanca Highway km 28, Matanzas (23°11′N, 82°04′W), C.J. Finlay leg. Feb. 1959, Finlay collection, specimen 15.—Same, km 27 (23°11′N, 82°05′W), C.J. Finlay, leg., 1951–1956, Finlay collection, specimens 5,9,10,11, ANSP 359101, specimens 13,14. Puerto Rico: Punta Ostiones, 7 km S of Punta Guanajibo, W coast, 1 shell, April 22, 1949, 3 shells, May 22, 1949, G.L. Warmke, leg., ANSP, specimens 3–4, 17–18.—Ramey Air Force Base, NW coast, A. Phares, leg., ANSP, specimen 19.—Piñones Beach, 8–10 km E of San Juan, NE coast (18°26.8′N, 65°55.7′W), Mrs. D. Humphrey leg., 1970, Finlay collection, specimen 8. Virgin Islands: Hams Bay, St. Croix (17°47′N, 64°53′W), with 21 *E. phymanthi* shells, Feb.–March, 1957, G. Nowell-Usticke leg. AMNH 194365, specimen 38. Specimen 37 is the holotype. All remaining specimens except specimen 34 are paratypes.

A total of 38 specimens of *E. worsfoldi* was available for study. Of these, 6 were collected alive: 2 large specimens (the smaller the holotype), 2 juveniles, 1 with the dried body deep in the shell, and 1 with the operculum but no body. The last 2 and most of the remaining shells were collected from beach drift.

Many of the beach shells are in poor condition. The fairly fragile shell, predators (crabs? fish?), and wave action presumably are responsible. Out of the 38 shells, only 1 has an intact protoconch.

Natural history: At Grand Bahama, this species was found alive three times with *Stichodactyla helianthus* (Ellis and Solander, 1786), the preferred host also of *Epitonium albidum* (Orbigny, 1842)(Robertson, 1983b) and an occasional host of *Epitonium lamellosum*. Like *E. albidum*, *E. worsfoldi* was under the broad oral disc, next to the column, in sand. The holotype of *E. worsfoldi* was collected with an anemone that was either *Actinoporus elegans* Duchassaing, 1850 or *Homostichanthus duerdeni* Carlgren, 1900, a sand-dweller (Figure 18). Feeding (parasitism) on the anemones was not observed but must occur. The sand-agglutinated egg capsules are like those of *E. albidum* (Figure 19). The bathymetric range is 0–2 m.

CONCLUSIONS

The data in this paper are believed to warrant description of the two new Recent western Atlantic species. Their fossil ancestors seem not to be known in the Americas. As documented in the Appendix, the most similar Recent shells appear to occur in Japan and South Africa.

It will be noted in the Appendix that the 23 species have been assigned to a variety of genera and "subgenera" (many of the latter named by de Boury). *Epitonium worsfoldi* has characteristics of three of these "subgenera" combined. Epitoniid genera and subgenera need to be much more broadly based.

It is surprising that two such large, shallow water species in a well-collected area should have remained undescribed until now. They show the continuing role that amateurs play in collecting, observing, photographing, and providing material for systematic and biological studies in museums and marine stations. Amateurs not only find undescribed species on rare occasions but, perhaps more usefully, they can also make aquarium observations such as those of the Leemans reported here.

ACKNOWLEDGMENTS

Most of the specimens were collected by amateurs, and AMNH in the 1970's became the first museum to accession good specimens of one of the two species (from the Nowell-Usticke Collection). Other amateurs who contributed most to the discoveries by providing specimens, data, and photographs are Neal and Eleanor Leeman (formerly of Miami, Florida), C. John Finlay (formerly of Cuba), and Jack N. Worsfold (formerly of the Bahamas). Worsfold's Grand Bahama collection is now at ANSP. Dr. Frederick M. Bayer identified the *Phymanthus*, and Dr. Donald R. Moore helped the Leemans in various other ways. Dr. Norman D. Paschall and Helen DuShane were helpful in providing information. Dr. Daphne Gail Fautin identified the *Actinoporus* or *Homostichanthus* from figure 18 (no specimen was kept). The curators of the mollusk collections at MCZ, AMNH, and USNM helped by providing access to their collections and making loans. Other persons who helped with the loan or gift of specimens are Dr. Marvin R. Hyett, Mrs. Garwin (Marilee) McNeilus, Amy Phares, Colin Redfern, and Germaine L. Warmke. Mary Fuges inked figures 7, 8, and 13. Harriet Robertson calculated the mensural data and inked figures 9 and 17. Colin Redfern, Dr. Gary Rosenberg, Jack N. Worsfold, and two helpful reviewers read various drafts of the manuscript.

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APPENDIX.

Conchological comparisons or notes on 23 species similar to, or confused with *Epitonium phymanthi* and *E. worsfoldi*, regardless of provenance.

Scala amathusia Melvill & Standen, 1903:341, pl. 7, fig. 1. Kaicher, 1980: card 2300 [*Epitonium*]. Gulf of Oman. Smaller than *E. worsfoldi* (6.5 mm), with more whorls (8–9) for size.

Scalaria costulata Kiener, 1838–1839:5–6, pl. 2, figs. 4. Tryon, 1887:pl. 12, fig. 59. Robertson, 1963:57–58, pl. 5, fig. 4. Robertson, 1970:45 [identification confirmed]. DuShane, 1988:30–32, fig. 1 (ribs curiously opisthocline). ANSP 230639. Red Sea to Philippines. Thought to be a synonym of *S. principalis* (Pallas) by Sowerby (1844:88 bis), which he recorded from "Xipixappi, West Columbia." Larger (35.3 mm); spire high (spire angle 30°); suture slightly disjunct; up to 28 ribs on last whorl; umbilicus narrow, deep.

Scalaria crassa Sowerby, 1844:91 bis, pl. 33, fig. 55. Kaicher, 1981: cards 3066, 3081 [*Epitonium*]. Philippines. Unlike *E. worsfoldi*, ribs unequal, slightly fewer (18) at largest size; may be spirally brown-banded.

Epitonium (*Limiscala*) *crypticocorona* Kilburn, 1985: 309–310, figs. 79, 126. South Africa. Smaller (7 mm); weak "coronation" inside suture; 12–19 ribs; low spiral lirae.

Scalaria dubia Sowerby, 1844:90 bis, pl. 33, fig. 41. Not *Epitonium dubium* Röding, 1798:92. Sowerby in Reeve, 1873: species 45, 45b wrongly as 75b. Tryon, 1887: 60, pl. 12, figs. 67–68. De Boury, 1912:95–97, pl. 7, fig. 4. Kilburn, 1985:327. Type species of *Foliacciscala* de Boury, 1912. ANSP 19573 (broken); USNM G.177. Australia, Samoa, etc. Larger (37 mm); spire angle 45°; like *E. phymanthi* but lacks crests; ribs very low, thin, slightly recurved, rarely enlarged, up to 42 on last whorl; suture impressed but not disjunct; spiral threads crowded, variable; last whorl inflated; umbilicus very narrow.

Scala emiliae Melvill & Standen, 1903:343–344, pl. 7, fig. 6. Kaicher, 1980: card 2313 [*Epitonium*]. Kilburn, 1985:307, figs. 120–121. Pakistan to South Africa. Smaller than *E. phymanthi* (12 mm); spire slightly higher (spire angle 40°); 21–36 low, thread-like ribs; pale brown (if not faded).

Scalaria friabilis Sowerby, 1844:95 bis, pl. 33, fig. 74. Kaicher, 1980: card 2329 [*Epitonium*]. Southern Australia. Higher spire than *E. phymanthi* (spire angle 30°–35°); spire profile evenly convex; no umbilicus.

Scala frielei Dall, 1889:313. Not illustrated. USNM 83727 (syntypes); AMNH 194388. North Carolina; Virgin Islands. Clench & Turner (1952:300–301) and Warmke & Abbott (1962:81, pl. 14a) misidentified this species. Smaller (6.4 mm); 24–31 ribs on last whorl; no shouldering; strong spiral threads; umbilicus narrow; spire fairly high (spire angle 45°). *Epitonium phymanthi* has been misidentified as this species.

Epitonium (*Nitidiscala*) *hancocki* DuShane, 1970:332, pl. 51, fig. 1. DuShane, 1974:32–33, fig. 73. Kaicher, 1983: card 3612. Galápagos. Smaller (13 mm); spire higher (spire angle 30°); fewer ribs (21); rib crests wavy.

Scalaria imperialis Sowerby, 1844:91–92 bis, pl. 33, figs. 56–57. Wilson & Gillett, 1972, pl. 13, figs. 5, 5a [color]. [*Epitonium imperiale*]. Kaicher, 1980: card 2304. AMNH 136625, 157310; ANSP 181726, 195661, 253841, 253842, uncat.; MCZ 294909, 294914; USNM 694170. East Africa, Western Australia, Philippines and Queensland. Larger (40 mm); pale tan to dark reddish or purplish brown, commonly in spiral bands (ribs white); more ribs, increasing to 48 on last whorl; umbilicus wide and deep; operculum grey-black.

Scalaria irregularis Sowerby, 1844:90 bis, pl. 33, figs. 40, 60. Philippines; Japan. USNM 343440. Up to 18 mm long; spire angle 65°; ribs crowded, 37 on last whorl, irregular in thickness but generally thin, with slight cresting; strong spiral threads; slightly umbilicate; 1 pale brown subsutural band present or absent on white. Resembles *E. phymanthi*.

Scalaria kraussi Nyst, 1871:116. Kilburn, 1985:293–295, figs. 97–100 [*Epitonium* (*Hyaloscala*)]. +*Epitonium shepstonense* E.A. Smith, 1910:204, pl. 7, fig. 15. Kaicher, 1981: card 3113. South Africa. Smaller (10–16 mm); spire averages higher (spire angle 25°–40°); 17–37 fine, low, erect or slightly reflexed ribs on later whorls; umbilicus closed. Species believed to be most similar to *E. worsfoldi*.

Perlucidiscala lacrymula Jousseaume, 1911:198, pl. 5, figs. 37–42. Kaicher, 1981: 3063 [*Epitonium* "*lachrymula*"]. Gulf of Aden. Smaller (5 mm); spiral threads towards apex.

Scalaria latifasciata Sowerby *in* Reeve, 1874: species 117. Type species of *Papyriscala* de Boury. Taki, 1956 [anatomy]. ANSP 70738, 219307, 234733, 243255; MCZ 294908 and 5 uncat. lots. Mozambique; Mauritius; Japan. Up to 18 mm long; spire low (spire angle 55°); trace of whorl disjunction; thin, low ribs mostly not connected from whorl to whorl; 32 ribs on last whorl, some irregularly spaced or thickened; weak to strong spiral threads; no crests; 2 or 3 brown spiral bands; slightly umbilicate.

Scalaria lincolata "Kiener" Sowerby, 1844:91 bis, pl. 33, figs. 45, 46, 48. Confused with *S. lineata* Kiener not Say. Nyst, 1871:118, pl. 2, fig. 5, pl. 6, fig. 20. Kaicher, 1981: card 3125 [*Epitonium*]. ANSP 70742, 86246, 243289; MCZ 294911 and 2 uncat. lots; USNM 198709. Gulf of Aqaba; Mauritius; Philippines; Japan. Up to 19 mm long; spire angle 40°; ribs more numerous (16–33) and more irregularly spaced and thickened ribs; no spiral sculpture; umbilicate; 1–3 brown spiral band(s) per whorl; operculum dark brown.

Scalaria lyra Sowerby, 1844:89 bis, pl. 32, figs. 38–39, pl. 34, figs. 81–82; Sowerby *in* Reeve, 1873: species 23.

Kaicher, 1980: card 2341 [*Epitonium*]. Kilburn, 1985: 308–309, figs. 122]. ANSP 19566, 19567, 119638; MCZ 187720; USNM 431817, 306339; 820891. Type species of *Limiscala* de Boury. Fiji to Japan and the Red Sea to Mozambique. Slightly smaller (20+ mm); spire lower (spire angle 60°); 27–45 erect ribs; spiral threads fine and dense; 0, 2 or 3 brown spiral bands.

Scala melior Melvill & Standen, 1903:345, pl. 7, fig. 9. Kaicher, 1980: card 2333 [*Epitonium*]. ANSP 164808 (syntype); USNM 424868. Pakistan; Gulf of Oman. Smaller (6.5 mm+); 8 (teleoconch?) whorls; spire angle 30°; up to 23 ribs per whorl; spiral threads present or absent. Resembles a small *E. worsfoldi*.

Scala micromphala Mörch, 1875a:258 ("Vieques," Puerto Rico, one specimen collected by A.H. Riise). Not illustrated. Photograph of holotype in Clench and Turner (1951:258–260, pl. 112, fig. 3), wrongly synonymized by them with *E. occidentale* Nyst, 1871, which according to them has "12 to 15 costae on the body whorl." According to Mörch there were 18 ribs on the 5 mm.-long shell. An *E. phymanthi* that long would have had more than 20 ribs. In addition, *E. micromphala* has subsuturally crested ribs; in *E. phymanthi* the crests are on the shoulders of the ribs. Mörch wrongly likened *S. micromphala* to *S. imperialis* (see under that species).

Scala (*Viciniscala*?) *minuticosta* de Boury, 1912:87–90, pl. 7, fig. 1. Compared with *Scala costulata* and *S. principalis*. "West Columbia." DuShane (1974:20–22, figs. 20–26). Larger than *E. worsfoldi* (35 mm); spire high (spire angle 35°); 21 mainly thin, low ribs on last whorl; whorls all narrowly disjunct, but ribs attached; traces of spiral striae; umbilicus narrow, deep; ribs slightly reflexed; crowded spiral threads.

Turbo principalis Pallas, 1774. Nomen dubium. *Epitonium principale* (Pallas) Röding, 1798:91. De Boury, 1912:89–90, 97. See above in synonymy of *E. worsfoldi*.

Scalaria robillardi Sowerby, 1894:42–43, pl. 4, fig. 5. Kaicher, 1981: card 3037. Kilburn, 1985:305–307, figs. 118–119 [*Epitonium* (*Papyriscala*)]. Red Sea and India to South Africa. Smaller (15 mm); more ribs (20–24 on last whorl); umbilicate; pale tan with 2–3 brown spiral bands (rarely absent).

Epitonium shepstonense. See above under *E. kraussi*.

"*Foraceiscala*" [=*Foliaceiscala*] *virgo* Masahito & Habe, 1976.172, figs. 2–3. Compared with "*Foraceiscala*" *dubia* (Sowerby, 1844). Japan. Paratype most resembles *E. phymanthi*; spire angle 40°; 50–60 weakly lamellate growth riblets; suture slightly disjunct, whorls connected by ribs; aperture constricted (holotype); oblique spiral threads.

Epitonium (*Nitidiscala*) *willetti* Strong & Hertlein, 1937:171, pl. 35, fig. 5. DuShane, 1974:38–39, fig. 72. Tropical eastern Pacific. Much smaller (3.2 mm); 18–22+ ribs.

Phalium (Semicassis) vector, a New Deep-Water Species from the Central Indian Ocean

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ABSTRACT

Phalium (Semicassis) vector, a new species of the family Cassidae, is described from the Saya de Malha Bank, northeast of Mauritius in the Indian Ocean. It differs from its closest relative, *Phalium microstoma* (von Martens, 1903) from Somalia, in having a lighter, less elongate shell with stronger beads on the spiral lirae.

Key words: Cassidae, Saya de Malha Bank, Indian Ocean.

INTRODUCTION

A number of new species of marine mollusks have been collected over the past few years by Soviet research vessels exploring the Saya de Malha submarine bank in the central part of the Indian Ocean. Among these are species of cassids not known at the time of my revision of this family (Abbott, 1968).

In 1975, Kilburn described *Phalium glabratum* subspecies *fernandesi* from deep water off Somalia. Two years later it was dredged by the R/V Gordy on the Saya de Malha Banks. With it were recovered at least five specimens of a new *Phalium* referable to the subgenus *Semicassis* Mörch, 1852.

The bathymetry and geology of the Saya de Malha Bank are discussed by Bouchet and Bail (1991:161), while Bondarev and Röckel (1992) provided an excellent popular account of this bank, which is located along the Mascarene Ridge north of the Mauritius and Cargados Carajos Shoals (between 9°30′S and 12°20′S, and 59°30′E and 62°30′E).

SYSTEMATICS

Phalium (Semicassis) vector Abbott, new species
Figures 1–2

Synonymy:

Phalium sp. 1, Bondarev & Röckel, 1992:28,32, fig. 5.

Description: Shell (fig. 1) reaching 60 mm in length, light, strong, evenly ovate, with numerous, fine, flattish, crowded, weakly-beaded spiral lirae separated by sunken interstices of equal width. Color opaque white with large, faint, light-brown blotch on dorsal surface of last whorl. Protoconch (fig. 2) of 3½ whorls, obtuse-conical, glassy-white, smooth. Teleoconch of 5½ whorls, the last bearing 23 flattish, spiral cords with fine beads at intersections with fine axial threads. Suture simple, slightly impressed. Spire convex-conic. Aperture ⅔ shell length. Outer lip reflected, of variable thickness, enamel-white, crossed by 20–22 distinct, sharp white denticles. Both true and false umbilici small, open, deep. Channel behind siphonal canal deep, narrow. Parietal wall slightly glazed over. Anterior part of columella strongly and unevenly pustulose, inner edge with 4–5 small denticles, outer edge with 3–4 small, rounded projections. Soft parts and operculum unknown.

Type locality: Central Basin, Saya de Malha Bank, Mascarene Ridge, northeast of Mauritius, Indian Ocean, dredged from sandy silt bottom at a depth of 80 meters, R/V Gordy, 1989. More precise locality data did not accompany the holotype.

Material examined: Holotype, USNM 860326, Paratypes 1–3, Donald Dan collection, all from the type locality. The specimen illustrated by Bondarev and Röckel (1992: fig. 5) is designated as paratype 4.

Etymology: I take pleasure in naming this species after the first recreational diving vessel to operate under the Russian flag, the *Vector*.

Comparative remarks: This new species belongs to a species group of *Phalium (Semicassis)* mainly limited to

Table 1. *Phalium (Semicassis) vector* new species. Linear shell measurements (mm) and counts.

	Length	Width	Number of whorls
Holotype	53.6	32.0	7
Paratype 1	56.8	32.1	8
Paratype 2	53.4	33.4	7
Paratype 3	60.0	33.5	9

Figures 1, 2. *Phalium (Semicassis) vector* new species. **1.** Apertural, lateral, and dorsal views of the holotype. 1.0 X. **2.** Protoconch of paratype 1. Both from Saya de Malha Bank, Mascarene Ridge, N. E. of Madagascar, dredged from sandy silt bottom at a depth of 80 meters, R/V Gordy, 1989. Scale bar = 500 μm

the western Indian Ocean, although similar species, such as *P. sculptum* J. de C. Sowerby, 1840 (Miocene), *P. mekranicum* (Vredenburg, 1925) (Upper Miocene) and *P. oligocalanticum* (Vredenburg, 1925) (Oligocene) have been reported from fossil beds on the mainland of India.

Phalium vector most closely resembles the eastern African deep-water *Phalium (Semicassis) microstoma* (von Martens, 1903), from which it differs in being much lighter in weight, less elongate, and in having stronger beads on the spiral lirae. *Phalium vector* lacks the four or five spiral brown bands on the body whorl, but instead has a faint tan blotch on the dorsal surface of the body whorl. The very weak, rounded projections on the outer, left edge of the columella of *P. vector* are reminiscent of the fingertip projections found in the shallow-water Indian Ocean *Phalium faurotis* (Jousseaume, 1888).

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Férussac and d'Orbigny's "*Histoire naturelle générale et particulière des Céphalopodes acétabulifères*": Dates of Publication of Plates and Text

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ABSTRACT

Férussac and d'Orbigny's "*Histoire naturelle générale et particulière des Céphalopodes acétabulifères*" is an essential contribution to teuthology, because of the numerous new species described, and because it represents the first important compilation of cephalopods. Issued between 1834 and 1848, in 21 livraisons, the actual dates of publication of most of its parts were hitherto uncertain. A thorough bibliographic search has allowed us to gather new information about the publication of this work. We can now identify and date precisely the 30 plates issued in 1834 and the 72 plates issued in 1835; the remaining 42 plates are dated 1839–1841 or 1839–1842. D'Orbigny's text was issued between 1839 and 1848 (livraison 12–21). The last three livraisons (1845–1848) included only text.

Key Words: Cephalopods; Publication dates; Férussac and d'Orbigny.

INTRODUCTION

During the first half of the 19th Century, a vast amount of material was collected by the scientists participating in French voyages around the world, the accounts of which were published under the following titles: *Voyage aux terres Australes* (*le Géographe*, *le Naturaliste*, *la Casuarina*) from 1800 to 1804 by Péron; *Voyage de la Coquille*, from 1822 to 1825 by Lesson; *Voyage en Amérique méridionale*, from 1826 to 1833 by d'Orbigny; *Voyage autour du monde* (*Uranie et Physicienne*), from 1817–1820 and *Voyage de l'Astrolabe*, from 1826 to 1829 by Quoy and Gaimard; *Voyage de la Bonite*, from 1836 to 1837 by Eydoux and Souleyet. The specimens collected on all of these voyages were deposited in the Muséum National d'Histoire Naturelle, Paris, and described not only by the collectors themselves, but also by other contemporary zoologists such as de Blainville, Lamarck and Férussac. These collections gave rise to numerous works that constitute a considerable contribution to the development of natural history.

The publications issued during the first half of the 19th century were delivered as a series of numbered parts, or livraisons, and several years were often necessary to complete a work. Such is the case for the "*Histoire naturelle générale et particulière des Céphalopodes acétabulifères. . .*" by Férussac and d'Orbigny, which was issued in 21 livraisons, from 1834 to 1848, and whose publication was particularly lengthy and confused.

Férussac intended to publish an important and general work on Mollusca ("*Histoire naturelle, générale et particulière des Mollusques*"), where all the monographs written by him and other authors might be included. As early as 1825, he had asked d'Orbigny to collaborate in the publication of the "*Histoire des Céphalopodes*". D'Orbigny started at once to produce plates and text, but in 1826 he left for an eight year long voyage to South America. It was only in 1834–35, after his return, that the first parts were distributed. Férussac died in 1836, and it was not until 1837 that d'Orbigny could recover his manuscript, and he then spent the following two years updating it (1839: issue of the first part of d'Orbigny's text).

DESCRIPTION OF THE WORK

The "*Histoire naturelle générale et particulière des Céphalopodes acétabulifères. . .*" comprises 2 volumes bound according to the instructions of d'Orbigny:

1—A volume of text, starting with d'Orbigny's Preface (pp. I-LVI), followed by 361 pages of taxonomic descriptions. The first livraison of text (livr. 12) is dated 1839 and largely postdates the Atlas.

An introduction to Mollusks and general remarks on Cephalopods by Férussac (96 pages), was issued in liv-

raisons 1 to 6 (1834–1835). A copy of this text was consulted at the "Bibliothèque Nationale" in Paris, where it is kept in the original wrapper, on the cover of which appears: "*Histoire naturelle générale et particulière des Mollusques—Monographie des Céphalopodes Cryptodibranches*". This part was originally intended to be included in the work, but d'Orbigny considered it to be obsolete. In his instructions to the binder he specifies that it is not part of the work on the Cephalopods and must therefore be bound separately.

2—An Atlas of 144 plates (90 plates named "Cryptodibranche", 52 named "Acétabulifère", one bearing both names (Octopus pl.23) "Cryptodibranche" and "Acétabulifère", and one having neither of them (Bellerophon pl.7).

Winckworth (1942) stated that a large number of plates were ready in 1826, when d'Orbigny left for South America; but were delivered only after his return in 1834. Férussac was at that time publishing the "*Histoire naturelle . . . des Mollusques terrestres et fluviatiles*" in collaboration with Deshayes. He also had to assume the heavy costs of the "*Bulletin Universel des Sciences et de l'Industrie*", which he created and managed. However, Férussac (1831:374) himself confirms that most of the "Cryptodibranche" plates were ready in 1831: "*depuis longtemps tous les Céphalopodes de l'ordre des Cryptodibranches . . . composent cet ouvrage prêt à être livré à l'impression, et dont les planches au nombre de près de 80 sont tirées et enluminées*".

HISTORICAL ACCOUNT OF PREVIOUS RESEARCH

Sherborn and Woodward (1901:75) were the first to publish some dates, in a footnote to their paper on the publication dates of "*Mollusques terrestres et fluviatiles*" by Férussac and Deshayes. They are very concise and do not mention their sources: "Of the dates of publication of this work all that can at present be said is that the first three out of 21 liv. appeared in Sept. 1834, nos.4–9 in 1835, no.12 in 1839, nos.13–18 in 1840 taking the work up to p. 240; and that it was finished in 1848".

The copy of Férussac and d'Orbigny's work in The Natural History Museum, London, gives some evidence of how Sherborn deduced some of the dates. A handwritten note says:

"It is obvious, as the date 1837 occurs on pp. III + 27 & 1838 on pp. V + 73 & 1839 on p. 139—that no text was published before 1837. 9 parts were published by 1835 (clearly these were all plates or part of the text to volume II Atlas, which containing no species does not concern us). Part 12 was published in 1839 & 13–18 (bringing the work up to p. 240) in 1840. A fresh font of type was used on p. 241 (compare the 444's in the pagination) & references to 1845 are frequent between pp. 241–361.

I therefore regard Vol. I, pp. I-LVI & 1–240 as 1840; pp. 241–361 as 1848; Vol. II text, pp. 1–96 as 1835".

These considerations are dated October 1901. The last part is repeated in the bibliography of the Index Animalium (Sherborn, 1922: LIII), with an extra remark: "[Dates] of plates unknown".

The references to 1835 most probably come from the *Bibliographie de la France*, which he thouroughly consulted to date Férussac and Deshayes' "*Histoire naturelle des Mollusques. . .*". He thus probably knew that the first 9 livraisons were issued in 1834 and 1835, and that they comprised only plates (although he did not know which ones) and Férussac's preface.

Thus Sherborn did not have sufficient information to date the plates, but he attempted to date the text, relying on the dates cited in the first pages of the text and in the preface by d'Orbigny. His conclusion was that the text could not have been issued before 1837 (he had no data regarding livraisons 10 and 11).

As far as the dates of livraisons 12 (1839) and 13–18 ("bringing the work up to p. 240"; 1840) are concerned, we could not determine his sources. He stated that a fresh type font was used on p. 241, in the pagination, but after a thorough examination of the different copies we could consult, we noticed that such a change in the pagination font of type actually occurs on page 273.

Winckworth (1942) had some additional data that allowed him to propose dates for the plates issued in 1834–1835. He possessed a bound copy of the 1834–1835 livraisons, although he did not have enough information to know precisely if this copy represented 9, 10 or 11 livraisons, and which of the plates were issued in 1834 and which were issued in 1835.

For the text, he used:

- the dates proposed by Sherborn and Woodward (1901);
- d'Orbigny's "*Mollusques vivants et fossiles*" (1845), a thorough reading of which allowed him to point out that all the plates and the text up to and including page 271 are mentioned. This led him to introduce an extra break in the text, and to date as 1848 all the text following page 271;
- the text of d'Orbigny himself, where 1839 is the latest bibliographic reference on page 210, and where the "*Mollusques vivants et fossiles*" (1845) is first mentioned on page 273;
- the indications on the back wrappers of the "*Histoire. . . des mollusques terrestres et fluviatiles*", with which he, however, partly disagrees. This is discussed in more detail below.

ORIGINAL RESULTS AND DISCUSSION

Three articles issued in the "*Bulletin zoologique*" and in the "*Annales des Sciences naturelles*" enlightened us as to the content of the first livraisons, and encouraged us to investigate further and to retrace the history of the publication of the "*Histoire générale et particulière des Céphalopodes Acétabulifères*". Successively, the following data were gathered from 11 different sources:

1—"*Bibliographie de la France, ou Journal général de l'Imprimerie et de la Librairie*". Paris, Pillet Ainé:
23e année, no. 39, 27 Sept. 1834, p. 615, no. 5229;
24e année, no. 16, 18 Avril 1835, p. 246, no. 2099;
no. 23, 6 Juin 1835, p. 360, no. 3058.

The issue, number of pages of text and plates of livraisons 1–9, are announced but no details are given on the content of the livraisons: Livraisons 1–3 (27 September 1834): 30 plates and 5 sheets of text; livraisons 4–6 (18 April 1835): 29 plates and 7 sheets of text; livraisons 7–9 (6 June 1835): 25 plates and 1 sheet with front page.

2—"*Bulletin Zoologique*", 2e section, 1835:
- p. 14–16: some details on livraisons 1–3 are given;
- p. 63–65: all the species figured in the plates of livraisons 4–6 are listed.

3—"*Annales des Sciences naturelles*", 2e série, 3, Zoologie. Paris, Crochard 1835, p. 192 (f.12, March). As early as March 1835, 12 livraisons of 9 to 10 plates each are announced as ready, 9 of which were on sale (whereas *La Bibliographie de la France* announces their issue later in the same year). A list of all the species issued in the plates of the livraisons 1–9 is given.

4—"*Notice analytique sur les travaux de Zoologie de Mr. Alcide d'Orbigny*" (1856). Duméril made two favorable reports at the Académie des Sciences, on the first eleven livraisons, on the 15 December 1834 and 29 June 1835 (see also d'Orbigny's Introduction, p. II). This allows livraisons 10–11 to be dated 1835.

5—"*Registre des procès-verbaux et rapports des séances de l'Académie Royale des Sciences. Institut*", vol.10, 1832–1835: p. 579, 22 September 1834: the delivery of Férussac's first three livraisons is announced; p. 724, 29 June 1835: Duméril indicates that the last five livraisons are issued.

In the "*pochette de la séance du 15 décembre 1834*" we found Duméril's report (two handwritten pages) describing the first three livraisons, i.e. an Introduction by Férussac and 28 plates ("*les figures de l'animal de l'Argonaute argo et de son anatomie, faites par Poli ... lithographiées par Chazal. Plusieurs espèces nouvelles de poulpes, et des dessins exécutés à Cadix d'après les dissections de deux très habiles anatomistes ... reproduites par Jacob*".

There is no trace in the "pochette" of Duméril's report on the 29 June 1835, concerning the "last five livraisons".

Our sources are consistent with livraisons 1 to 11 being delivered in 1834–1835, the first nine three by three. The "last five livraisons" announced by Duméril in 1835 are thus livraisons 7–9 and 10–11.

6—"*La littérature française contemporaine, 1827–1844, Dictionnaire Bibliographique*" by MM. Ch.Louandre and F. Bourquelot, Paris, Félix Daguin, t.3, 1848, p. 190–191. The "*Histoire ... des Céphalopodes*", is announced as published in Paris, 1834–1842, in 20 livraisons, each comprising 10 plates and corresponding text, 18 livraisons of which were on sale. Thus we did deduce that 18 livraisons were issued from 1834 to 1842, livraison 18 being dated 1842; we know that the last livraison (21st) was issued in 1848. From the evidence of the type font change on p. 273 and of references to d'Orbigny (1845), we consider that livraison 20 (pp. 273–320, see below) also appeared in 1848. As for livraison 19, we date it 1845, since apparently it was not yet on sale in 1844, but the text up to p. 271 is quoted by d'Orbigny (1845).

7—Two complete works (Text and Atlas) from the "*Bibliothèque Nationale*": their peculiarity is that they have been marked with different stamps (Bibliothèque Impériale, Bibliothèque Royale or Bibliothèque Nationale). All the plates are stamped, whereas the text bears only a few stamps. A thorough examination of these stamps in the two volumes of text revealed that they were not randomly distributed but seemed to correspond either to the beginning or to the end of a set of livraison (Table 1).

In one of the copies of the Atlas, all the plates are marked "*Bibliothèque Royale*", except 32 that are stamped "*Bibliothèque Impériale*". These 32 plates correspond to most of the plates that we consider as belonging to livraisons 1–3. We conclude that the latter set constitutes a homogenous lot, which can be dated 1834, except for 4 plates of *Argonauta*, which we are sure belong to livraisons 7–9 (*Bull.Zool.* 1835 and *Ann.Sci.nat.* 1835).

All the plates in the second Atlas are stamped "*Bibliothèque Royale*", except 46 that are marked "*Bibliothèque Nationale*" (BN). Knowing what is included in the first 9 livraisons, and from what we infer is included in livraisons 10–11 (confirmed by our source no. 8), we deduce that the stamp "*Bibliothèque Nationale*" was used for all the plates of livraisons 4–6, for almost all the plates of livraisons 10–11 and for one plate of livraisons 7–9.

8—An incomplete bound copy of the work present at the National Museum of Wales, the title page of which is "*Histoire naturelle générale et particulière des Mollusques*", contains the *Introduction and general remarks on Cephalopods* by Férussac, and 101 plates. It corresponds perfectly to the first 11 livraisons, issued in 1834–1835, as detailed in the preceeding paragraphs. Only one discrepancy was observed: plate 25 of *Octopus*, printed by Benard and stamped as BN, that we consider to be part of the livraisons 10–11, is not included in this copy.

The National Museum of Wales also has a complete copy with handwritten notes by Hoyle, and a series of 77 plates, unbound, corresponding to an incomplete set of livraisons 1 to 11. Plate 25 of *Octopus* is present in this last series of plates.

9—The complete copy present at The Natural History Museum, London, bears two handwritten notes. One, by Sherborn on the first page of vol.I (Text), dates the text. Its content has been discussed above. The other, by E.A.Smith on the first page of vol.II (Atlas), says: "Mr.Sherborn has been unable to discover anything definite with regard to dates of publication of any of these plates".

Table 1. Details of text livraisons, with all available information on the sheets of each livraison, inclusion (P) or not in the BIMM copy, the stamped pages in the two complete works (1 and 2) at the BN and the probable date of issue. BR = Bibliothèque Royale; BN = Bibliothèque Nationale.

Sheets	Pages/stamps	Number of sheets	P = BIMM copy	Livraison	Year
1–6	1/BR1–48	6	P	12	1839
7–12	49/BR1–96/BR1	5		13	1839–41
13–18	97/BR1 + BR2–144/BR1	5		14	1840–41
a–c	I/BR1–XXIV	5	P	15	1841
19–20	145–160/BR1				
21–24	161/BR1–192/BR1	4	P	16	1841
25–29	193/BN1 + BR2–232/BR1	5	P	17	1841
d–g	XXV/BR1–LVI	4	P	18	1842
30–34	233/BN1–272	5		19	1845
35–40	273/BN1–320	6		20	1848
41–45	321/BN1–361	5		21	1848

10—An incomplete bound copy of the work, from the library of the "Laboratoire de Biologie des Invertébrés marins et Malacologie" (BIMM) at the Museum National d'Histoire Naturelle (MNHN) comprising: the introduction and preface by d'Orbigny (pp. I-LVI), the text p. 1–48 and 145–232, 30 plates, all coming from the same printer (Imp. Lemercier, Benard et C.).

We interpret this BIMM copy as corresponding to livraison 12 (pp. 1–48) and livraisons 15–18 (pp. I-LVI; 145–232), i.e. five livraisons, each of 4 to 6 sheets of text and 6 plates (livraison 17 is announced on back wrappers as comprising 5 or 6 sheets of text and 6 plates). This interpretation also takes into account the observations on the other copies of the work.

There remain 12 plates of the Atlas that belong neither to the first 11 livraisons nor to the BIMM copy. Printed well before the text, they are thought to have been issued in livraisons 13–14 (i.e. two livraisons of 6 plates each).

Thus all the plates were delivered before 1845 (citations in d'Orbigny, 1845). The livraisons 19, 20 and 21 include only text.

11—"*Notice analytique sur les travaux zoologiques et paléontologiques de Mr.Alcide d'Orbigny*" (1844). D'Orbigny states that his manuscript was finished in 1839. However, later, the death of the publisher interrupted the printing of the text, and caused several trials. This accounts for the gaps in the publication of livraisons from 1842 to 1845, and from 1845 to 1848.

TEXT

The data gathered from the incomplete BIMM copy, together with the stamps on the text in the two complete copies of the BN have led us to propose that the text was issued in 10 livraisons.

Livraison 12, pp. 1–48, 1839. This livraison is included in the incomplete copy of the BIMM. The first page is stamped "Bibliothèque Royale" in the BN. Its issue is announced on the back wrappers of "*Mollusques terrestres et fluviatiles*" (Winckworth, 1942). After three years without any livraison being issued, it seems obvious that d'Orbigny, who had started to rewrite his manuscript in 1837 (cf. Introduction p. III), had published the initial part of it in this livraison. It also seems evident that the Introduction, which cites works issued in 1840–1841, cannot have been issued in 1839.

Livraison 13, pp. 49–96, 1839–1841. The stamp "Bibliothèque Royale" occurs on the first and last page of this livraison, which constitutes 5 sheets. Further supporting evidence is that this livraison is not included in the incomplete BIMM copy. The announcements on the back wrappers of "*Mollusques terrestres et fluviatiles*" (Winckworth, 1942) state that 16 livraisons were issued in 1839–1841. Lacking any further information, we date livraison 13 as 1839–1841.

Livraison 14, pp. 97–144, 1840–1841. The stamp "*Bibliothèque Royale*" is on p. 97 of both copies in the BN, and also on p. 144 in one of these copies. The break at page 97 is thus confirmed twice. The incomplete BIMM copy lacks pages 49–144, confirming the end of the livraison. A reference to 1839, on p. 139, allows livraison 14 to be dated 1840–1841.

Livraison 15, Introduction, pp. I-XXIV, and text pp. 145–160, 1841. This livraison is included in the BIMM copy, and is stamped on p. I and p. 160 of the BN copy. Stamps in the text corresponded to a livraison of only two sheets, which seemed insufficient to us. When the first part of the introduction is included, a livraison of 5 sheets is obtained, stamped at the beginning and at the end. This is consistent with the issue of the Introduction in two separate livraisons (stamps on p. I and on p. XXV). References to publications issued in early 1841, as well as indications on the above-quoted wrappers lead us to propose the date of 1841 for livraison 15.

Livraison 16, pp. 161–192, 1841. This livraison is included in the BIMM copy. The BN copy is stamped at the beginning (p. 161) and at the end (p. 192). Livraison 16 was issued between two other livraisons of 1841 and is therefore dated 1841.

Livraison 17, pp. 193–232, 1841. This livraison is in-

Table 2. Publication dates of the Atlas plates, with identification of the corresponding livraison. Pl = plate number; stp = stamps on the Bibliothèque Nationale copies; BI = Bibliothèque Impériale; BN = Bibliothèque Nationale.

	Pl	stp	Livraison	Date
Octopus	1	BI	1–3	(1834) 1826
	2	BI	1–3	22 Sept. 1834
	3	BI	1–3	22 Sept. 1834
	3/2°	BI	1–3	22 Sept. 1834
	4	BI	1–3	(1834) 1826
	5	BI	1–3	22 Sept. 1834
	6	BI	1–3	22 Sept. 1834
	6/2°	BI	1–3	22 Sept. 1834
	6/3°	BI	1–3	22 Sept. 1834
	7	BI	1–3	22 Sept. 1834
	8	BI	1–3	22 Sept. 1834
	9	BI	1–3	22 Sept. 1834
	10	BI	1–3	22 Sept. 1834
	11		7–9	1835
	12	BI	1–3/4–6	22 Sept. 1834
	13	BI	1–3/4–6	22 Sept. 1834
	14	BN	1–3/4–6	22 Sept. 1834
	15	BN	1–3/4–6	22 Sept. 1834
	16	BN	7–9	March 1835
	17		7–9	March 1835
	18	BN	10–11	29 June 1835
	19	BN	10–11	29 June 1835
	20	BN	10–11	29 June 1835
	21	BN	13–14	1839–41
	22	BN	10–11	29 June 1835
	23		13–14	1839–41
	24	BN	10–11	29 June 1835
	25	BN	10–11	29 June 1835
	26		12/15–18	1839–42
	27		13–14	1839–41
	28		13–14	1839–41
	29		13–14	1839–41
Eledone	1	BI	1–3	22 Sept. 1834
	1/2°	BI	1–3	22 Sept. 1834
	2	BI	1–3	22 Sept. 1834
	3		12/15–18	1839–42
Argonauta	1	BI	1–3	22 Sept. 1834
	1/2°	BI	1–3	22 Sept. 1834
	1/3°	BI	1–3	22 Sept. 1834
	1/4°	BI	1–3	22 Sept. 1834
	1/5°	BI	1–3	22 Sept. 1834
	2	BI	7–9	March 1835
	3	BI	7–9	March 1835
	4	BI	7–9	March 1835
	5	BI	7–9	March 1835
	6		12/15–18	1839–42
Bellerophon	1	BI	1–3	22 Sept. 1834
	2		12/15–18	1839–42
	3		12/15–18	1839–42
	4		13–14	1839–41
	5		12/15–18	1839–42
	6		12/15–18	1839–42
	7		12/15–18	1839–42
Cranchia	1	BN	4–6	March 1835
	2		7–9	March 1835
Sepiola	1	BI	1–3	22 Sept. 1834

Table 2. Continued

	Pl	stp	Livraison	Date
	2		7–9	March 1835
	3		12/15–18	1839–42
	4		12/15–18	1839–42
Sepia	1	BN	4–6	March 1835
	2	BN	4–6	March 1835
	3	BI	1–3	22 Sept. 1834
	3/2°	BN	4–6	March 1835
	3/3°	BN	4–6	March 1835
	4		7–9	March 1835
	4/2°		7–9	March 1835
	5	BN	4–6	March 1835
	5/2°		7–9	March 1835
	6		10–11	29 June 1835
	6/2°		10–11	29 June 1835
	7		7–9	March 1835
	8		7–9	March 1835
	9		10–11	29 June 1835
	10		7–9	March 1835
	11	BN	10–11	29 June 1835
	12	BN	10–11	29 June 1835
	13	BN	10–11	29 June 1835
	14		12/15–18	1839–42
	15		13–14	1839–41
	16		13–14	1839–41
	17		12/15–18	1839–42
	18		12/15–18	1839–42
	19		12/15–18	1839–42
	20		12/15–18	1839–42
	21		12/15–18	1839–42
	22		12/15–18	1839–42
	23		12/15–18	1839–42
	24		12/15–18	1839–42
	25		12/15–18	1839–42
	26		12/15–18	1839–42
	27		12/15–18	1839–42
Sepioteuthis	1	BN	4–6	March 1835
	2	BN	4–6	March 1835
	3	BN	4–6	March 1835
	4	BN	4–6	March 1835
	5	BN	10–11	29 June 1835
	6		12/15–18	1839–42
	7		12/15–18	1839–42
Loligo	1C	BI	1–3	22 Sept. 1834
	1A	BN	10–11	29 June 1835
	2	BN	4–6	March 1835
	3	BN	4–6	March 1835
	4	BN	4–6	March 1835
	5	BN	4–6	March 1835
	6		7–9	March 1835
	7		7–9	March 1835
	8		7–9	March 1835
	9		7–9	March 1835
	10		7–9	March 1835
	11	BN	4–6	March 1835
	12	BN	4–6	March 1835
	13	BN	7–9	March 1835
	14	BN	4–6	March 1835
	15		7–9	March 1835
	16	BN	4–6	March 1835
	17	BN	4–6	March 1835

Table 2. Continued

	Pl	stp	Livraison	Date
	18		10–11	29 June 1835
	19		7–9	March 1835
	20		13–14	1839–41
	21	BN	10–11	29 June 1835
	22		12, 15–18	1839–42
	23		13–14	1839–41
	24		13–14	1839–41
Loligopsis	1	BN	4–6	March 1835
	2		7–9	March 1835
	3		7–9	March 1835
	4		13–14	1839–41
Onychoteuthis	1	BI	1–3	22 Sept. 1834
	2	BN	4–6	March 1835
	3	BN	4–6	March 1835
	3/2°	BN	4–6	March 1835
	4	BN	4–6	March 1835
	5	BN	4–6	March 1835
	6	BN	10–11	29 June 1835
	7	BN	10–11	29 June 1835
	8	BN	10–11	29 June 1835
	9	BN	10–11	29 June 1835
	10	BN	10–11	29 June 1835
	11	BN	10–11	29 June 1835
	12		12, 15–18	1839–42
	13		12, 15–18	1839–42
	14		12, 15–18	1839–42
Ommastrephes	1		12/15–18	1839–42
	2		12, 15–18	1839–42

cluded in the BIMM copy. Both BN copies are stamped at the beginning (p. 193), and one of them also at the end (p. 232). It is comprised of 5 sheets. The back wrappers of "*Mollusques terrestres et fluviatiles*" (1841), state: "*la 17ème livraison sera mise en vente à la fin d'août*" (Winckworth, 1942:35). The date and content of this livraison are given as 5 to 6 sheets of text and 6 plates. Our conclusions concerning this livraison contradict Winckworth, who disbelieved the announcement on the back wrappers.

Livraison 18, Introduction pp. XXV-LVI, 1842. Page XXV is stamped in the BN copy. This livraison is included in the BIMM copy. This second part of the Introduction comprises 4 sheets. We include it in livraison 18 since we know that livraison 17 was made of 5 or 6 sheets. The date 1842 is given by Louandre and Bourquelot (1848) and is supported by five of our sources.

Livraison 19, pp. 233–272, 1845. This livraison is not included in the BIMM copy. It is stamped on the first page (p. 233) in the BN copy. The date 1845 is based on the fact that livraison 19 is not mentioned as issued in the analyses of the "*Littérature française*" of the period from 1827 to 1844 (Louandre & Bourquelot, 1848), but the pages of this livraison are quoted in "*Mollusques vivants et fossiles*" d'Orbigny (1845).

Livraison 20, pp. 273–320, 1848. This livraison is not included in the BIMM copy. It is stamped on the first page (p. 273) in the BN copy. A different type font was used for the pagination, starting on p. 273 (especially the 5's). References to the "*Mollusques Vivants et Fossiles*" (1845) appear in the text, confirming that this livraison was published after 1845. It was probably issued with the 21st livraison in 1848.

Livraison 21, pp. 321–361, 1848. This livraison is not included in the BIMM copy. The BN copy is stamped on the first page (p. 321). "*Mollusques Vivants et Fossiles*" (1845) is cited in this livraison. It is the last livraison, and is undoubtedly dated 1848.

ATLAS

The "*Bulletin Zoologique*" and the "*Annales des Sciences Naturelles*" list all the species figured in the plates issued in livraisons 1–9. The incomplete copy at Cardiff gathers the first eleven livraisons, as detailed in sources 2, 3, 8 (see above). Plates included in the BIMM copy (source 10; livraisons 12 and 15–18) could not be dated more precisely than 1839–1842.

Details concerning the dates of publication and the corresponding livraison of each plate are summarized in table 2. Our conclusions concerning the issue of the Atlas are as follows:

Livraisons 1–3, 22 September 1834: 30 plates.

Livraisons 4–6, March 1835: 29 plates (4 of which were already issued in livraisons 1–3).

Livraisons 7–9, March 1835: 25 plates.

Livraisons 10–11: 29 June 1835: 22 plates.

Livraison 12, 1839: 6 plates.

Livraisons 13–14, 1839–1841: 12 plates.

Livraisons 15–18, 1841–1842: 24 plates.

Two plates issued in livraisons 1–3 (*Octopus* pl.1 and 4) had been distributed as early as 1826 by d'Orbigny himself (footnote p. 18: "*A la fin de 1825, nous avons fait lithographier nos planches représentant les figures de l'Octopus Cuvierii* et de l'*O.Leehenaultii*, et elles ont été distribuées à beaucoup de personnes").

CONCLUSIONS

A comparative analysis of Férussac and d'Orbigny's work and that of d'Orbigny (1845) confirms that the dates quoted by d'Orbigny are not reliable. As an example, *Cranchia* plate 1 includes three species: *C. cardioptera*, *C. minima* and *C. scabra*. In d'Orbigny (1845), they are cited as figured in plate 1, and dated respectively 1826 (p. 390), 1830 (p. 351) and 1839 (p. 240). Such inaccuracy is common in d'Orbigny's dates, and was often the case at that time.

Our bibliographic searches allowed us to acertain the precise dates of issue of the 102 plates of the Atlas that were issued in 1834 and 1835, as well as their composition. The dates of issue of the remaining plates are 1839–1842 (livraisons 12–18), but we can find no details on the actual content of each livraison.

In the publication of the text, we recognize three main stages:

1. 1834–1835. Livraisons 1–11: Introduction and general remarks by Férussac. 102 plates of the Atlas. No descriptions.

2. 1839–1842. Livraisons 12–18: Introduction and general remarks by d'Orbigny. Text pp. 1 to 232. Atlas: the remaining 42 plates.

3. 1845–1848. Livraisons 19–21: last part of the text, pp. 233–361. No plates.

The above data and conclusions are summarized in two tables. Table 1 provides information concerning the livraisons of text and corresponding dates. Table 2 provides the publication date for each plate, and associates the plate with a corresponding livraison.

ACKNOWLEDGMENTS

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Alvania valeriae (Gastropoda: Rissoidae), a New Species from off Southeastern Brazil

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ABSTRACT

Alvania (*Punctulum*) *valeriae* new species, is found off the coast of Rio de Janeiro and Espírito Santo States, southeastern Brazil. It differs from other species of *Alvania* occurring off the Brazilian coast in having more numerous axial ribs (about 36 on the body whorl). Axial ribs are more pronounced than the 12–14 spiral threads, and nodules are not formed at their intersections.

Key words: Gastropoda, Rissoidae, *Alvania*, Brazil

INTRODUCTION

Alvania (*Punctulum*) *valeriae* new species was collected on the continental shelf off Rio de Janeiro and Espírito Santo States, in dredgings taken during the oceanographic operations Espírito Santo I (July to September, 1984), and Cabo Frio VII (March to July 1983), as part of routine sampling by the Brazilian Navy to obtain basic oceanographic data on the coastal and oceanic regions off Brazil. The malacofauna found during these operations was characterized by numerous small mollusks, among which the Rissoidae were prominent (Absalão, 1989).

The first descriptions of rissoids that occur off Brazil, or would later have their ranges extended to Brazilian waters, are those of d'Orbigny (1842), Watson (1886), who studied the material collected by the H.M.S. Challenger, and Dall (1889), who worked with material collected by U.S.S. Blake (Romer & Moore, 1988). Since 1966, malacological material from off the Brazilian coast has been obtained on a more regular basis, thanks to the dredging operations of the Brazilian Navy (Absalão, 1986). The minute specimens (< 5 mm) have received almost no attention. The Rissoidae especially "have proved to be very difficult to classify at all levels because of their small size, diverse form, and confusion caused by convergence, especially in shell characters" (Ponder, 1985). Abbott (1974) stressed that the entire group was in need of revision before species could be assigned to subgenera. The revision of Coan (1964) was mainly a bibliographic compilation. Ponder (1985) made the last and most complete revision of this family at the generic level.

ABBREVIATIONS

IBUFRJ = Instituto de Biologia da Universidade Federal do Rio de Janeiro, Brazil.
MORG = Museu Oceanográfico da Fundação Universidade de Rio Grande, Brazil.
USNM = National Museum of Natural History, Smithsonian Institution, USA.
MZUSP = Museu de Zoologia da Universidade de São Paulo, State of São Paulo, Brazil.
MNUFRJ = Museu Nacional do Rio de Janeiro, State of Rio de Janeiro, Brazil.
MNHN = Museum National d'Histoire Naturelle (Paris), France.

SYSTEMATICS

Family **Rissoidae** H & A. Adams, 1854

Genus *Alvania* Risso, 1826

Type species: *Turbo cimex* Linnaeus, 1758.

There are three previously described species of *Alvania* that occur off the Brazilian coast: *A. auberiana* (Orbigny, 1842), *A. deliciosa* Jeffreys, 1884 and *A. xanthias* (Watson, 1885). The first occurs in shallow waters and the latter two at greater depths.

Alvania (*Punctulum*) *valeriae* Absalão, new species
(figures 1–3)

Description: Shell minute, 1.6 to 2.4 mm long, white ovate-conic, with rounded whorls. Suture well impressed, slightly canaliculated. Protoconch multispiral, smooth,

with 2½ whorls. Apical angle 52–65°. Teleoconch with about 36 gently curved axial ribs and 12–14 spiral threads on body whorl. Axial ribs override spiral threads without forming nodules at intersections. Base rounded with 6–8 spiral threads. Intritacalx present over entire teleoconch. Terminal varix absent. Umbilicus small, chink-like, well defined. Operculum and radula unknown.

Type locality: Off southeastern Espírito Santo State, southeastern Brazil (20°38′12″S, 40°16′12″W), 38 m depth, 22.5°C and 36.7 ppt salinity, Brazilian Naval Research Vessel ALMIRANTE SALDANHA, station 6449, August 23, 1984.

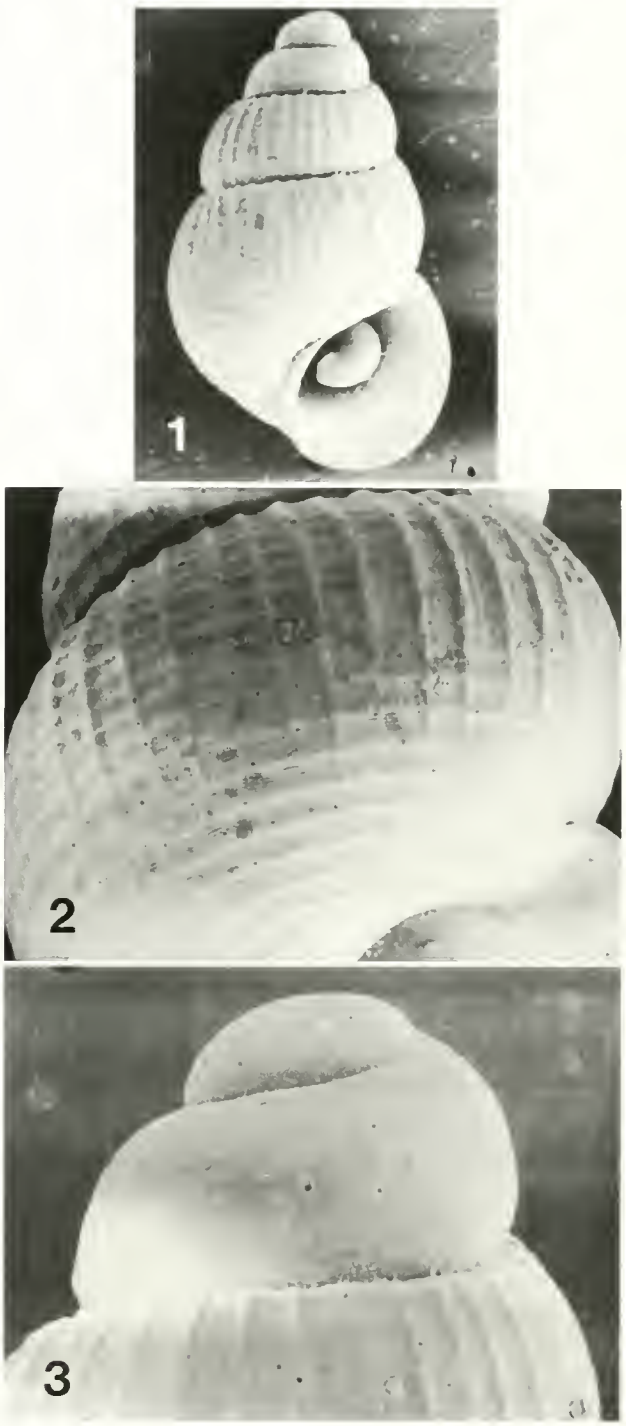
Type material: Holotype IBUFRJ 1726, 1.74 mm height, 1.02 mm width. Paratype 1, MORG 26986 off northeastern Rio de Janeiro State, Brazil (23°08′18″S, 41°03′18″W), 85 m depth, 16.7°C and 36.2 ppt salinity, ALMIRANTE SALDANHA, station 6417, August 29, 1984, 1.80 mm height, 1.04 mm width. Paratype 2, USNM 860503, off northeastern Rio de Janeiro State, Brazil (22°35′00″S, 40°50′00″W), depth 77 m, 19.2°C and 36.1 ppt salinity, ALMIRANTE SALDANHA, station 6422, August 16, 1984, 1.80 mm height, 1.04 mm width. Paratype 3, MZUSP 27716, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C and 35.5 ppt salinity, March 29, 1983, 1.80 mm height, 1.04 mm width. Paratype 4, MNUFRJ 5978, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C, and 35.5 ppt salinity, March 29, 1983, 2.40 mm height, 1.28 mm width. Paratype 5, IBUFRJ 1727, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C, and 35.5 ppt salinity, March 29, 1983, 2.16 mm height, 1.20 mm width. Paratype 6, MORG 27681, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C, and 35.5 ppt salinity, March 29, 1983, 1.88 mm height, 1.04 mm width. Paratype 7, MORG 27682, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C, and 35.5 ppt salinity, March 29, 1983, 1.80 mm height, 1.04 mm width. Paratype 8, IBUFRJ 1728, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, depth 92 m, 15.6°C, and 35.5 ppt salinity, March 29, 1983, 2.00 mm height, 1.12 mm width. Paratype 9, MNHN, off Rio de Janeiro State, Brazil (23°16′50″S, 43°02′40″W), ALMIRANTE SALDANHA station 6174, March 29, depth 92 m, 15.6°C, and 35.5 ppt salinity, 1983, 1.84 mm height, 1.08 mm width.

Etymology: This species is dedicated to my wife, Mrs. Valéria Gomes Veloso.

Range: Records of *A. valeriae* are restricted to the region between northern Rio de Janeiro State and southern Espírito Santo State, southeastern Brazil.

Discussion: *Alvania colombiana* is compared to *A. valeriae* because both species occur in the same biogeographic region. However, they are not sympatric. As *Alvania* is largely a European group, comparisons with those warm-water species were included.

Alvania auberiana, *A. deliciosa* and *A. xanthias* have respectively 14, 14 and 12–14 axial ribs, whereas *A. valeriae* has 32–40 ribs. This character alone is sufficient to discern it from the other species occurring in Brazilian



Figures 1–3. *Alvania valeriae* new species. **1.** Holotype, IBUFRJ 1727; 120×. **2.** Ornamentation details, 240×. **3.** Protoconch, 240×.

waters. In addition, *A. auberiana* has 5 spiral threads on its teleoconch, *A. deliciosa* has 10, *A. xanthias* has only 4 spiral threads that are restricted to the base, whereas *A. valeriae* has 12–14 spiral threads (figures 1 and 2) on its teleoconch.

Alvania colombiana Romer and Moore, 1988 differs from *A. valeriae* in having only 26 axial ribs, which disappear on the base of the shell, and 7–9 spiral grooves. *Alvania valeriae* has ≈36 (32–40) axial riblets that extend only slightly over the body whorl without reaching the umbilical region of the shell, as well as 12–14 spiral threads.

Alvania porcupinae (Jeffreys, 1884) has a smooth protoconch very similar to that of *A. valeriae*, ≈32 axial ribs that disappear smoothly towards the umbilical region, while *A. valeriae* differs in having ≈36 (32–40) axial ribs that enter a little beyond the edge of the penultimate whorl. The diameter of the last two whorls increases greatly in *A. porcupinae*, but little in *A. valeriae*.

Alvania zylensis Gofas and Warén 1982, and *A. imperspicua* Palary, 1920 can be easily distinguished from *A. valeriae* on the basis of protoconch sculpture. The protoconch of *A. valeriae* is smooth, that of *A. zylensis* has 12 zigzag spiral lines that intersect, forming a reticulated pattern, while that of *A. imperspicua* has 7–8 spiral lines that also zigzag but do not intersect. In addition, *A. imperspicua* has protruding nodules on the teleoconch, which are formed by the junction of axial riblets and spiral lines. In contrast, *A. valeriae* lacks such nodules.

Although *A. valeriae* is similar in shape to *A. compacta*, this latter species has fewer axial riblets (20–30) and spiral threads (6–8) than the former, which has ≈36 (32–40) axial riblets and 12–14 spiral threads. *Alvania compacta* also has nodules where axial and spiral ornamentation cross.

Alvania valeriae is unique among its southwestern Atlantic congeners in having a large number of axial ribs that clearly dominate the 12–14 spiral threads.

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Protoconch Size Variation Along Depth Gradients in a Planktotrophic *Epitonium*

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ABSTRACT

The protoconch length of *Epitonium echinaticosta* ranges from 330 to 790 μm in the northern Bahamas. The length increases along depth gradients from near 0 m to 40–52 m. Intermediates are from intermediate depths. One planktotrophic species is involved. A possible explanation is given. Systematists should be aware that the phenomenon may occur in other planktotrophic epitoniids or other marine prosobranchs.

Key words: *Epitonium*, protoconch, size variation.

INTRODUCTION

> ". . . the protoconch may provide the best guide to relationships [within the Epitoniidae] yet. Of course ecological factors . . . may prove to influence protoconch form (as has been established in other gastropod groups) but this remains to be shown for the Epitoniidae." Kilburn, 1985: 241.

There is scattered mention in the literature on marine prosobranch gastropods of one species having protoconchs that differ from shallow and "deep" water. None of these cases seems to have been documented with measurements, descriptions and illustrations. In some cases different species perhaps were involved.

In this paper, I show that in a single planktotrophic species of *Epitonium* much variation in protoconch size occurs in the northern Bahamas. Size (length) increases with increasing depth (and possibly also with exposure to wave action). Populations from Grand Bahama sampled from 9, 10, 24, and 40 m, and from 11 and 52 m at Abaco all have larger protoconchs than do those from nearby shallow sites (0–2 m).

The epitoniid studied is *Epitonium echinaticosta* [not *echinaticostum*] (d'Orbigny, 1842) [type locality: St. Thomas, Virgin Islands; northern known limit: Bermuda (ANSP 100824); southern known limit: Fernando de Noronha, off Brazil (Leal, 1991)]. Because of its distinctive shell morphology, especially its variably disjunct and commonly "open" teleoconch coiling (Rex & Boss, 1976), and its 8–15 variably high and undulate axial ribs on the last whorl (Robertson, 1983b), Dall (1889) created for this species a subgenus *Cycloscala*, which has sometimes been ranked as a genus.

Species of *Cycloscala*, which occur in the Indo-Pacific as well as the western Atlantic, have been separated by degree of whorl disjunction and rib counts by de Boury (1911), Woodring (1928), Kilburn (1985) and DuShane (1990). Familiarity with a living population (Robertson, 1983a) clearly reveals that at least in the Bahamas there is just one species, with intergrades between the extremes, as concluded by Clench and Turner (1951). They recognized only one western Atlantic species of *Cycloscala*, and I concur.

In Bahamian *E. echinaticosta*, the frequencies of the different teleoconch coiling types vary little at different depths (Robertson, unpublished) and thus do not affect the conclusions here.

There is already some information about the coelenterate host, feeding and reproduction of *E. echinaticosta* in the Bahamas (Robertson, 1983a). At least in shallow water, the host is the actinian sea anemone *Bunodeopsis* [or *Viatrix*] *globulifera* (Duchassaing, 1850), commonly living on the leaves of turtle grass [*Thalassia testudinum* (Banks and Solander ex König)] (It also occurs on *Syringodium*, *Halimeda*, *Penicillus*, and *Acetabularia*.) The lower end of the bathymetric range of *E. echinaticosta* is given by Abbott (1974) as 200 fathoms (366 m). Whether living animals occur at that depth, and whether the *Epitonium* remains specific to *B. globulifera* are unknown. The *Epitonium* and anemone are most abundant in the Freeport canals.

How is it known that *E. echinaticosta* is planktotrophic? There is Leal's undocumented statement that off Brazil "planktotrophic development is indicated." More definitely, there is direct evidence of planktotrophy at least in Bahamian shallow waters: eggs of this species have been shown to be 98–106 μm in diameter (mean = 102 μm; n = 10)(Robertson, 1983a). Two swimming veligers, admittedly abnormal, were seen to hatch naturally from egg capsules (Robertson, 1983a).

Table 1. Locality data, repositories of vouchers, water depths, and protoconch lengths of *Epitonium echinaticosta* from Grand Bahama, Abaco, Bimini and the Berry Is., all northern Bahamas. Data are arranged in order of increasing depth. Abbreviations: ANSP = The Academy of Natural Sciences of Philadelphia, CR = Colin Redfern collection, GB = Grand Bahama; n = numbers of specimens measurable (out of many unmeasurable).

Localities	Vouchers (nos.)	n	Depths (m)	Lengths (μm)	
				Means	Ranges
Running Mon Canal, GB 26°29′45″N, 78°41′45″W	ANSP 367195 & 369759	16	1	370	330–430
North Hawksbill Creek, GB 26°32′00″N, 78°45′00″W	ANSP 370521	2	0–2	380	370–380
Silver Cove Canal, GB 26°30′30″N, 78°39′30″W	ANSP 367234 & 367235	23	1	410	370–470
Treasure Cove, Abaco 26°42′00″N, 77°18′20″W	CR 3990	1	0–2	450	
Chub Cay, Berry Is. 25°25′N, 77°54′W	ANSP 324293	2	0–2	450	440–460
South Bimini 25°42′N, 79°17′W	ANSP 325563	1	0–2	460	
Treasure Cay, Abaco 26°40′00″N, 77°18′15″W	CR 4598	1	0–2	510	
Settlement Point, West End, GB 26°42′15″N, 78°59′50″W	ANSP 372821	1	0–2	570	
Sandy Point, Abaco 26°00′15″N, 77°24′00″W	CR 3983	1	0–2	590	
Dead Man's Reef Beach, GB 26°34′45″N, 78°51′45″W	ANSP 367195	11	3–10?	550	470–640
Pinders Point, GB 26°30′30″N, 78°46′30″W	ANSP 370944 & 370521	1	9	640	
Kings Bay, Dundee Bay, GB 26°29′15″N, 78°43′30″W	ANSP 369074 & 369759	1	10	520	
Chub Rocks, Abaco 26°43′55″N, 77°13′05″W	CR 7638	4	11	650	610–740
Gold Rock, GB 26°30′00″N, 78°22′00″W	ANSP 369476	1	24	670	
Tamarind, GB 26°30′45″N, 78°36′00″W	ANSP 368803	1	40	660	
N of N.W. end (Great) Guana Cay, Abaco 26°44′N, 77°09′W	CR 5295 & 5296	3	52	760	730–790

> "The hatching shell diameter is about 170 μm, i.e. much larger than the egg. . . . The protoconch is about 0.3 to 0.4 mm long [small ones], i.e. it is much larger than the hatching veliger shell – proof that the larva grows substantially while in the plankton"

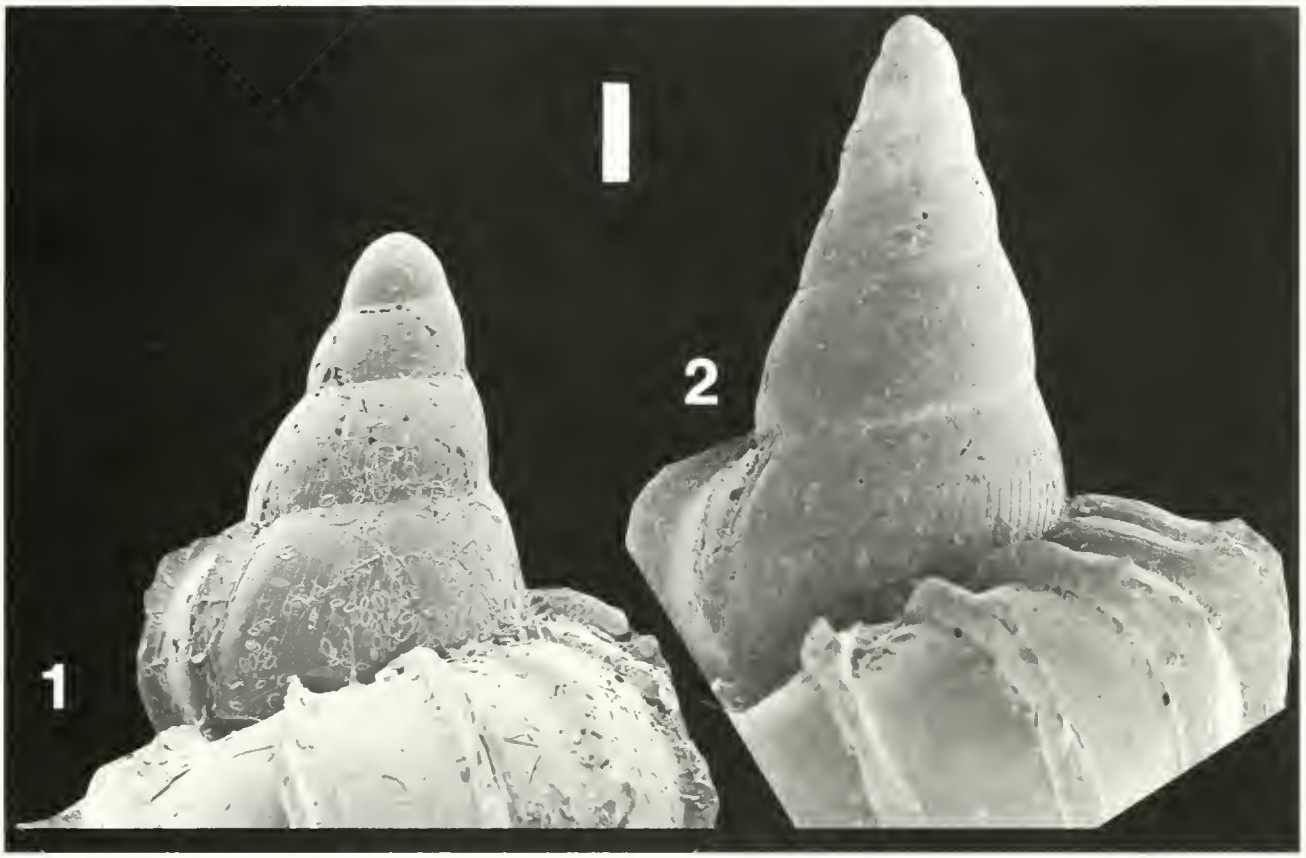
(Robertson, 1983a). There might be geographical variation, but the data from Abaco as well as Grand Bahama suggest that the larger protoconchs may grow in deeper water everywhere the species occurs.

In the literature, there is already an indication of protoconch size variation in another epitoniid. Two SEM photos of *Epitonium dallianum* (Verrill & Smith, 1880) protoconchs (Bouchet & Warén, 1986: figs. 1180–1181) show some intrapopulational shape and size variation. *E. dallianum* is deep-water and amphi-Atlantic in distribution.

Doubt has been cast on poecilogony (intraspecific variation in mode of reproduction) occurring in the Gastropoda, especially by Hoagland and Robertson (1988) and Bouchet (1989). Poecilogony usually refers to planktotrophy versus lecithotrophy. By extension, lack of poecilogony has been taken to mean that gastropod protoconchs are intraspecifically uniform in both form and size. This paper calls in question size specificity.

MATERIALS AND METHODS

This study is based on 68 live-collected and empty shells from shallow depths down to 40 m at southern Grand Bahama island (mainly in the canals of Freeport), 3 empty shells from 52 m off northeastern Abaco, Bahamas, 9 mainly beachworn shells from shallower depths at the same island, and a few also from Bimini and the Berry Islands, all in the northern Bahamas, all but the last two places on the Little Bahama Bank. The 52 m station was about 3240 m horizontally from the nearest shore.



Figures 1–2. SEM micrographs of protoconch and part of teleoconch of **1.** *Epitonium echinaticosta* from less than 2 m (Running Mon Canal, Freeport, Grand Bahama), with ca 3.5 protoconch whorls. Protoconch length = 410 μm. Teleoconch whorls sutured. **2.** *E. echinaticosta* from 52 m (off Abaco), with 5 protoconch whorls. Protoconch length = 770 μm. Note also the incised axial growth lines on both shells, an indication of planktotrophy. Teleoconch coiling of 2 was open, increasing the measured protoconch length only slightly. Scale bar = 100 μm for both micrographs.

Protoconchs were studied with light and scanning electron microscopy. Measurements were made to the nearest 10 μm with the aid of a calibrated ocular micrometer in a Wild dissecting microscope at ×50.

The anterior end of the larval shell is obscured to a varying degree by the first teleoconch whorl, which may or may not have disjunct coiling begining before, at, or after the protoconch varix. The length measurements were made on the exposed part of the protoconch, i.e. as far down as the protoconch varix (smaller than the first teleoconch rib) can be seen. Where the teleoconch becomes disjunct affects the length data slightly, but does not account for the differences in protoconch size reported here. Protoconch P's and first protoconch whorl diameters were too corroded to be measurable accurately (but a size estimate is given below under Results).

The originally 3 deep-water shells from Abaco are in the private collection of Mr. Colin Redfern (one was lost). Nine other voucher specimens from Abaco also belong to Redfern. Two other lots, from Bimini and the Berry Islands, are at The Academy of Natural Sciences of Philadelphia (ANSP). The rest, all from Grand Bahama and the Jack N. Worsfold Collection, are also at ANSP.

Data on each population studied are given in Table 1. No temperature or rearing data are available. The data are graphed on figure 4

RESULTS

First whorl diameters of both the small and large protoconchs are 100–140 μm (they approximate the egg sizes), and whorl numbers are 3.5 to 5. Whole protoconch widths of short and long larval shells are all 270–310 μm. Long and short protoconchs are similarly shaped (figures 1–2). All specimens have the usual planktotrophic *Epitonium* protoconch microsculpture (incised axial lines).

Protoconch lengths vary remarkably: from 330 to 990 μm. The smaller protoconchs have 3.5 to 4 whorls (figure 1) and the larger ones about 5 whorls (figure 2). Thus all are multispiral, another indication of planktotrophy. On the larger protoconchs, whorl numbers have increased, not whorl sizes.

The data from the two Freeport canal populations show that all protoconchs are very short but appear to be slightly different from each other in size, with populations from Running Mon having protoconchs no lon-

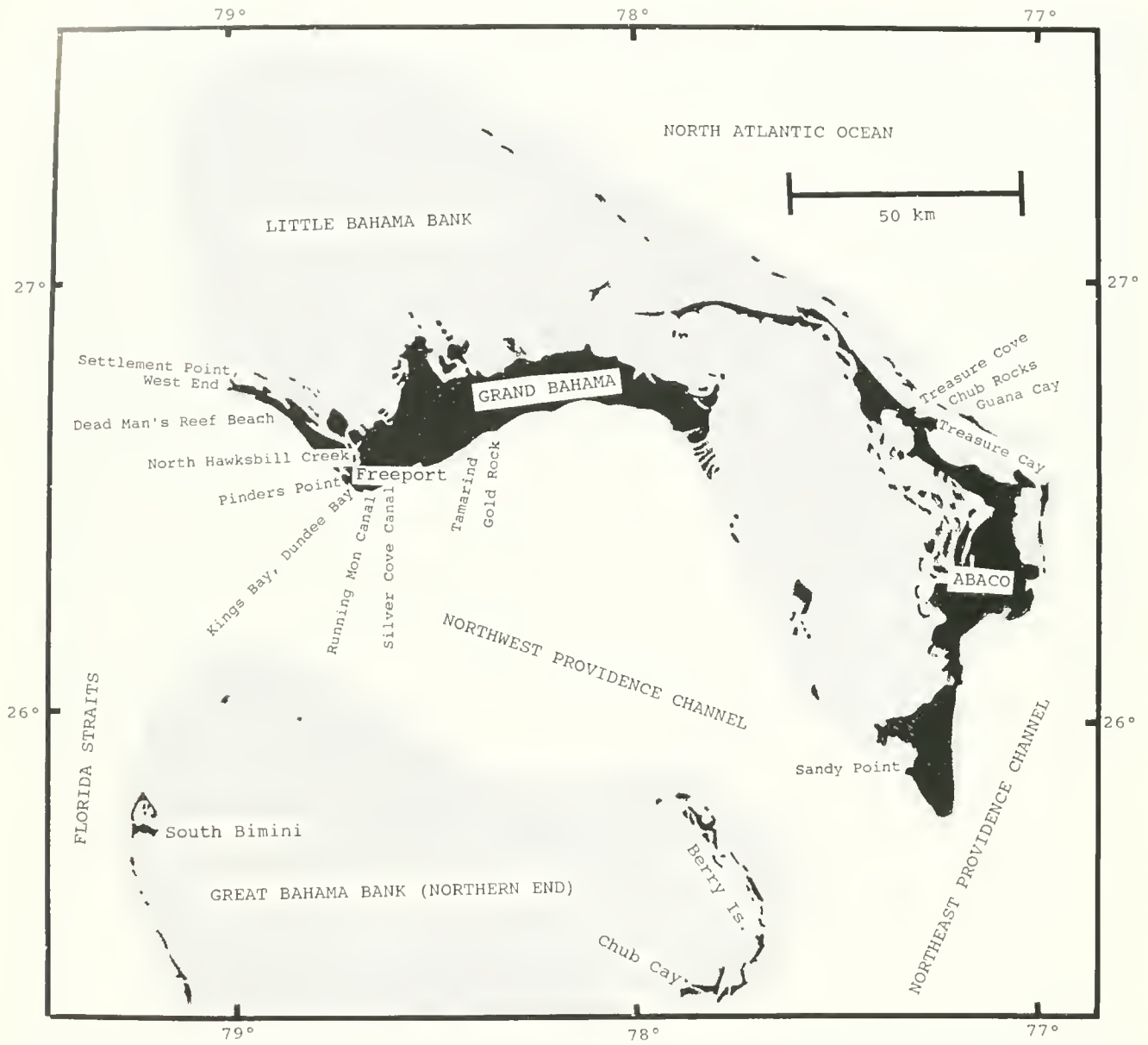


Figure 3. Map of the northern Bahamas, showing the Little Bahama Bank, part of the Great Bahama Bank and the localities in Table 1

ger than 430 μm and those from Silver Cove no longer than 470 μm.

The population sampled from Dead Man's Reef Beach is puzzling because it ranges in protoconch length from 470 to 640 μm, overlapping the largest shallow water shell from elsewhere and the smallest "deep" water shell. A possible explanation for the Reef anomaly is that the other two shallow localities are in sheltered canals, and the Dead Man's Reef is on the exposed south coast—where even near the surface, temperatures may be lower, exposure to wave action may be greater, and hosts may be more sparsely dispersed. The beach shells may have washed in from an estimated depth of 3–10 m beyond the near-beach reef.

Judging by the Chub Rock and Pinders Point samples, enlargement can occur in water as shallow as 9 and 11 m (Table 1). The Sandy Point shell has a moderately large protoconch (590 μm long) which can be explained by the presence of very deep water nearby (in the Northeast Providence Channel, figure 3), where greater exposure, colder shallow water and perhaps sparsely dispersed hosts can be expected.

The smallest Abaco protoconch (430 μm) is larger than the smallest Grand Bahama protoconch (330 μm). The Freeport canals have especially dense populations of *Bunodeopsis* (the anemone host).

DISCUSSION

Protoconch size bimodality in the Architectonicidae is probably genetic in origin (Robertson, 1970). Since the protoconch enlargement of Bahamian *Epitonium echin-*

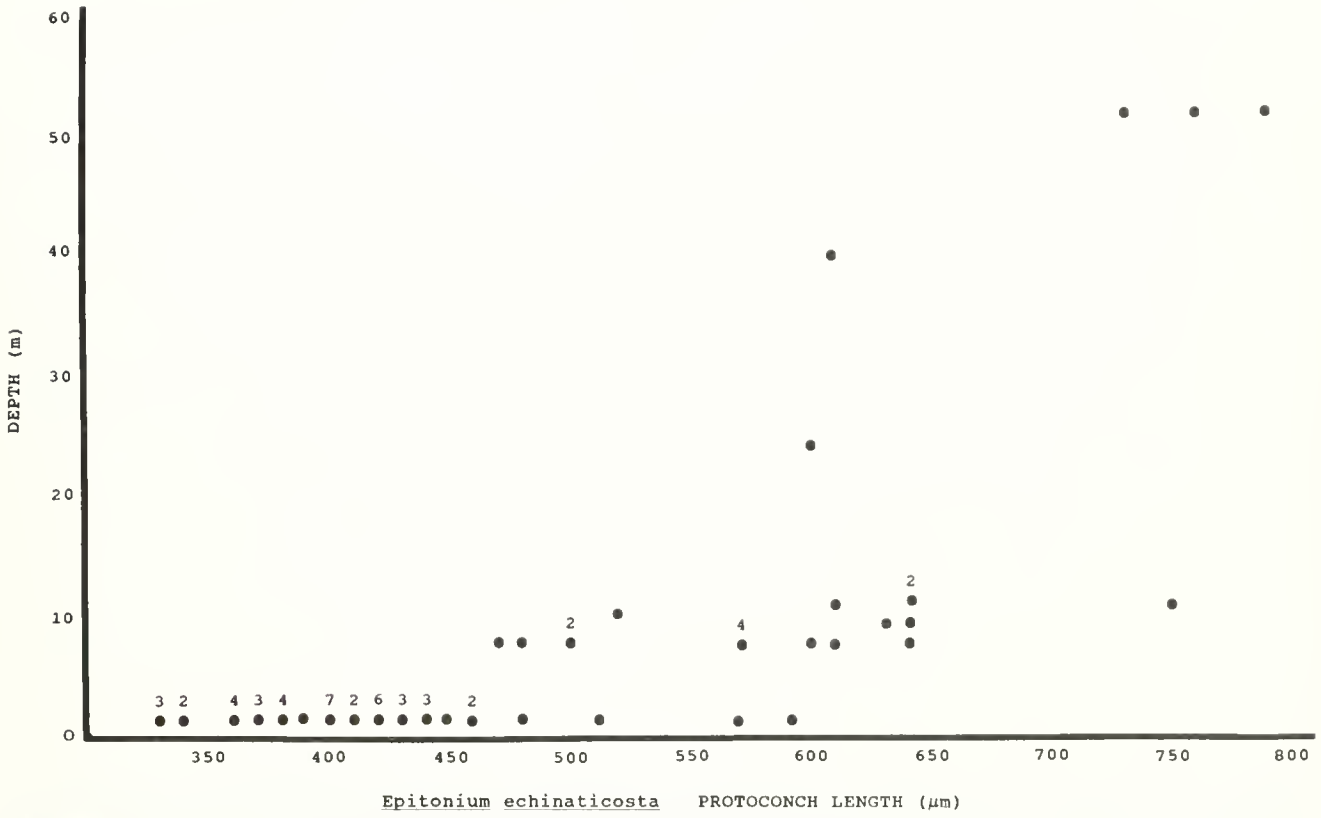


Figure 1. *Epitonium echinaticosta* protoconch lengths versus water depths. Data from Table 1. The spots with numbers show where two or more data points coincide.

aticosta at "depth" occurs in two areas more than 100 km apart (figure 3), an ecological rather than a genetic explanation seems necessary.

The factors most likely to account for the size variation of larval *Epitonium echinaticosta* are:

1. Duration of the pelagic larval stage. Movement to and fro by tidal and ocean currents.
2. Diurnal vertical migration of larvae such as reported in Mediterranean *Epitonium* spp. by Richter (1973, as *Scalaria*), who also recorded vertical distances traversed by other larval taxa in the order of 100 m.
3. Fast larval growth in the warm waters of the canals, slower growth near the cooler surface elsewhere, and slowest growth at "depth" in the coolest water. Scheltema (1967) and Pechenik (1984) showed experimentally that the larval growth rate in *Ilyanassa obsoleta* (Say, 1822) and *Crepidula fornicata* (Linnaeus, 1758), two other prosobranchs, responds to temperature in this manner.
4. In the absence of metamorphic cues, a long hypothesized delay period and continuing growth after the onset of competence. According to Pechenik (1986), the larval prosobranch *Bittium alternatum* (Say, 1822) can grow from 2.8–3.0 whorls to 3.7–3.8 whorls during the delay period. The minimum and maximum larval shell lengths at metamorphosis for *Crepidula fornicata* are 700 μm and 2300 μm (Pechenik, 1984).

The great abundance of *Bunodeopsis globulifera*, the sea anemone host of *Epitonium echinaticosta*, in the shallow, warm Freeport canals (the artificial equivalents of mangrove creeks) must be mentioned. Nearly all of the live-collected epitoniums are from the canals. There there is a large reproductive population of the *Epitonium* and it can be hypothesized that many of the larvae grow fast (in the warm water), swim near their parents, being moved back and forth by tidal currents, and settle and metamorphose promptly upon becoming competent (at small size, 3.5 whorls).

Outside the canals, the abundance of *Bunodeopsis* is not known. It is even possible that *E. echinaticosta* has one or more other coelenterate hosts at "depth." Some of the larvae in the sea could have come out of the canals but it is also probable that many were spawned outside. These larvae (from both sources) can be expected to drift into "deep" water and to undergo diurnal vertical migration, which would involve intermittent slow growth at "depth" (cool water), lateral movement in currents, and difficulty in finding host(s). The duration of the competent period is believed long, and large (5-whorled) larvae result.

Thus the duration of the pelagic larval stage is here considered the most likely factor bringing about the pro-

toconch size variation of *E. echinaticosta*. But factors 2–4 listed above must also be involved.

CONCLUSIONS

How widespread is this kind of variation among other mollusks? Partly allopatric and partly heterochronous size variation in the "protoconch" of the thecosome pteropod *Clio pyramidata* Linnaeus, 1767 has been reported in central and eastern North Atlantic Recent plankton and Late Pleistocene bottom deposits off northwest Africa by Diester-Haass and S. van der Spoel (1978). They attributed the variation to genetic influences, temperature differences, and "mixing of populations." Size differences are smaller than those recorded here and seem not to be comparable.

Long metamorphic delay periods, like those reported above in *Bittium* and *Crepidula*, seem a likely cause for the phenomenon to be widespread (little being known about prosobranch delay periods).

The prodissoconch sizes of some bivalves apparently are controlled by temperature (Lutz & Jablonski, 1978). As they pointed out, there could be paleoclimatological (or paleoecological) implications.

This seems to be the best documented case of extreme intraspecific protoconch size variation in one planktotrophic gastropod species, the variation probably induced by differing times in the plankton plus a long delay period (plus other factors). The variation is expressed bathymetrically. There is no indication that more than one *Epitonium* species is involved, or that there is poecilogony.

Ecophenotypic variation may be more frequent in marine mollusks than currently realized. Systematists should be alert to the phenomenon treated here and should beware of mere protoconch size differences for distinguishing planktotrophic species.

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Effect of Low Water Temperature on Ion Balance in the Zebra Mussel, *Dreissena polymorpha*, and the Unionid Mussel, *Lampsilis radiata*

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ABSTRACT

Dreissena polymorpha, acclimated to room temperature (21 ± 1°C) for 31 days in artificial pondwater, exhibits higher hemolymph sodium, chloride, potassium and total osmolarity than mussels acclimated to 4–5°C (cold), while hemolymph calcium was increased with cold treatment. The room temperature acclimated mussel hemolymph ion concentrations, maintained for 31 days in artificial pondwater, were similar to those measured from mussels sampled in the field. Cold-acclimation caused *Lampsilis radiata* hemolymph sodium, chloride and osmolarity values to decrease, while calcium and the "other" ions, presumably bicarbonate, increased. The positive net sodium and chloride flux and the calcium loss of zebra mussels acclimated to room temperature was reduced upon direct transfer into cold pondwater. Sodium and chloride net uptakes were increased in cold-acclimated zebra mussels with an acute increase in pondwater temperature while calcium and potassium net loss increased. The effects of cold storage on zebra mussels needs to be recognized due to possible changes in the physiology of the mussel with this treatment.

Key words: Cold-acclimation, ion flux, hemolymph ion concentrations, sodium, chloride, calcium, potassium

INTRODUCTION

The recently introduced zebra mussel, *Dreissena polymorpha*, has rapidly colonized the Great Lakes Region (Ontario Ministry of Natural Resources, 1992). Zebra mussels form large colonies of a high density, broadcast spawn, and have a veliger dispersal stage that remains in the water column for several weeks (Hebert, *et al.*, 1991; Mackie, 1991; McMahon, 1991; Garton & Haag, 1993). Aside from impacting industries and utilities by fouling or clogging water intakes and associated piping (Mackie, 1991; Kovalak *et al.*, 1993; LePage, 1993), zebra mussels also impact the ecology of their newly exploited regions by decreasing the density and diversity of freshwater bivalves of the family Unionidae (Hebert *et al.*, 1991; Hunter & Bailey, 1992; Mackie 1993) and by decreasing phytoplankton availability (Leach, 1993).

Animals in a freshwater habitat must regulate blood/hemolymph and cell ion concentrations above the environmental concentrations. Freshwater bivalves, while ionic hyperregulators for hemolymph and cell ionic components, have reduced concentrations of hemolymph and cell ions relative to other freshwater species. This results in a reduced overall ionic/osmotic gradient (Murphy & Dietz, 1976; Dietz, 1979; Kirschner, 1991). While hemolymph ion concentrations are low, fresh water mussel sodium and chloride transport rates compare favorably with those of other freshwater animals (Kirschner, 1983; Scheide & Dietz, 1986; Horohov *et al.*, 1992). The zebra mussel is similar to other freshwater mussels in such characters as relatively low hemolymph ion concentrations (Horohov *et al.*, 1992). Ion flux values for sodium and chloride in *Dreissena polymorpha* show a higher ion turnover with the net fluxes similar to those of other fresh water bivalves (Horohov *et al.*, 1992).

Current research protocols for long term storage of zebra mussels in the laboratory recommend that zebra mussels that are not used immediately be maintained at temperatures below 10°C (Reid *et al.*, 1993). The purpose of this study was to measure the effect of cold storage on ion balance in the zebra mussel and compare that response to a representative of the Unionidae. The net ion flux of zebra mussels was measured at two pondwater holding temperatures (room temperature and cold, 4°C). The effect of direct (acute) transfer from one temperature extreme to the other was also determined.

MATERIALS AND METHODS

Freshwater mussels, *Dreissena polymorpha* (Pallas, 1771) and *Lampsilis radiata* (Barnes, 1823), were collected from Lakes Erie, Huron and Michigan with ambient water temperatures ranging from 1 to 17°C. Zebra mussel sizes ranged from 13 to 35 mm. Zebra mussels were handled according to recommended zebra mussel containment procedures (Reid *et al.*, 1993). All laboratory water was of Nanopure grade (Barnstead). Large quan-

Table 1. A comparison of field collected, pondwater acclimated (51 days in the laboratory at room or cold temperatures) zebra mussel hemolymph ion concentrations.

	Concentration (mEq/liter)		
Ion	Room temp. pondwater acclimated	Cold temp. pondwater acclimated	Field collected
Sodium	20.2 ± 0.4	13.5 ± 1.2*	20.1 ± 1.0
Chloride	24.3 ± 0.9	18.0 ± 1.0*	20.4 ± 0.9*
Potassium	0.1 ± 0.1	0.2 ± 0.03*	0.5 ± 0.1
Calcium	3.4 ± 0.1	6.0 ± 0.1*	3.4 ± 0.2
Other	6.1 ± 1.6	7.1 ± 1.2	3.6 ± 0.9
Osmolarity**	54 ± 1	45 ± 2*	48 ± 2*

Values represent the mean ± the standard error of the mean
* Significantly different from the room temperature mussels ($P < 0.05$), n = 8 for both field and room temperature mussels and n = 16 for cold temperature acclimation mussels.
** Units in mOsmole/kg H_2O

tities of zebra mussels (greater than 100) were placed in at least 2 liters of artificial pondwater consisting of (mM/L): 0.5 NaCl, 0.4 $CaCl_2$, 0.2 $NaHCO_3$ and 0.05 KCl (Dietz & Branton, 1975). Mussels were divided into two groups. One group was maintained under laboratory conditions at room temperature with the water temperature ranging between 20–25°C. The other group was maintained at 4–5°C for at least 10 days prior to use. Both groups were maintained under constant light conditions. Mussels were not fed.

Mussel hemolymph was withdrawn from individuals by cardiac puncture (Fyhn & Costlow, 1975). Blood was centrifuged at greater than 14,000 Xg for 1 minute (IEC Centra M). Total osmolarity was determined using a Vapor Pressure Osmometer (Wescor, model 5500) with a 0, 12.5, 25, 50 and 100 mOsm/kg H_2O standard curve. Sodium, potassium and calcium were determined using flame photometry (Coleman Model 51 Ca Flame Photometer, Bacharach). Chloride was determined using a chloride titrator (Labconco). All ion determinations were referenced to commercially prepared standards and are expressed as mEq/L. The measured ions were totalled for each mussel and subtracted from the total solute osmolarity for each mussel. The difference is noted as "other" and assumed to be predominately bicarbonate (Horohov *et al.*, 1992).

Zebra mussel net ion flux, an indicator of ion balance, was determined using the methodology of Dietz and Branton (1975). Mussels were rinsed in deionized water for 30–60 minutes. The mussels were then transferred to beakers containing 10 ml artificial pondwater. At time zero, an arbitrary time chosen when the majority had opened and were siphoning following transfer, 4 ml of bathing media were withdrawn. After 4 hours, another sample of bathing media was withdrawn and the mussel tissue was removed from the shell and dried. The net flux of each mussel was calculated as the change in the bathing media ion concentration corrected for evaporative loss divided by mussel dry weight and time. The net flux is expressed as μEq/g•hr. A positive net flux indicates that the influx occurring during the experimental period was greater than the ion efflux. A negative net flux indicated that mussel ion efflux exceeded the influx for the experimental period.

All values are reported as the mean ± the standard error of the mean with the sample size noted (n). The Students 't' test was used to determine significant differences.

RESULTS

Mussels maintained in both temperature conditions were open and appeared to be siphoning, indicating normal mussel behavior patterns in each acclimation condition. Zebra mussels maintained in pondwater at room temperature had higher hemolymph sodium and chloride concentrations and therefore a higher hemolymph osmolarity than those mussels maintained in pondwater at 4 to 5°C (Table 1). The acclimation time for each zebra mussel group was 51 days. Hemolymph sodium concentrations decreased 26% in the cold treatment group ($P < 0.05$, n=8 for the room temperature group and n=16 for the cold group), while hemolymph chloride concentrations decreased 33%. Hemolymph potassium decreased 50% with the cold storage. Hemolymph calcium was increased 76% in the cold-acclimated mussels over room temperature-acclimated mussels. The observed osmolarity was 13% less in the zebra mussels maintained at 4°C compared to mussels maintained at room temperature, primarily reflecting the decrease in hemolymph sodium and chloride. The cold treatment did not significantly affect the "other" ions, presumably indicating no effect on bicarbonate.

Mussels acclimated 51 days at room temperature maintained hemolymph ion concentrations similar to the hemolymph concentrations of mussels sampled in the field (Table 1). Thus, *Dreissena polymorpha* can maintain ion balance during room temperature acclimation in artificial pondwater with values similar to animals found in the natural environment. This occurs in the absence of feeding.

To investigate whether the cold induced change in hemolymph ion concentrations was a specific characteristic of *Dreissena polymorpha* or common to other freshwater bivalves, the effect of a 10 day, cold acclimation on *Lampsilis radiata* was determined (Figure 1). Most of the trends observed with the zebra mussel were also observed in *Lampsilis*. Hemolymph sodium in *L. radiata* was reduced 60%, while the chloride concentration was reduced 75%. Hemolymph potassium remained similar between the two treatment groups. Hemolymph calcium was elevated 56% in *L. radiata* at the lower temperature. Hemolymph osmolarity was decreased 28% with the cold treatment. The remaining hemolymph ionic components ("other"), presumably bicarbonate, were elevated approximately 2 fold with cold treatment.

These data suggest that at least some freshwater bivalves may reduce their osmoregulatory "set point" in

cold temperatures as compared to mussels in warmer temperatures (laboratory temperatures). To test the effect of an acute temperature change on ion transport capabilities, zebra mussels were acclimated to either 21 ± 1°C water temperature or 4°C pondwater temperature for at least 10 days then tested at the other temperature. Mussels acclimated to room temperatures were observed to have a significant decrease in the sodium and chloride net fluxes, in magnitude and sign, when moved directly to the cold water ($P<0.05$, n= 14 mussels, room and cold temperatures except for the sodium flux room temperature mussels n=13, Figure 2). The negative sodium flux indicates a dominant efflux in the cold temperature testing condition whereas at room temperature the positive net sodium flux indicates a dominant influx. The negative sodium net flux was significantly different from zero ($P<0.05$, n= 14 mussels). The change in the net chloride flux was similar to that observed for the sodium net flux ($P<0.05$, n= 14 mussels, for room and cold temperatures). Interestingly, the direct transfer of the room temperature mussels into the 4°C pondwater resulted in a decrease in the magnitude of the calcium loss ($P<0.05$, n= 14, room and cold temperatures) indicating a decrease in the calcium efflux. The potassium loss, while being approximately one order of magnitude lower than the other ions, was significantly less in mussels transferred to the cold ($P<0.05$, n= 14, room and cold temperatures).

The comparison between zebra mussel net fluxes acclimated to cold pondwater and mussels acutely transferred to room temperature pondwater was similar to those acclimated to room temperature (Figure 3). Mussels, acclimated to the cold bathing media, had significantly lower sodium and chloride net fluxes than those directly transferred to room temperature ($P<0.05$ for sodium and chloride, n=16 mussels for both temperature groups). The sodium and chloride net flux in the cold-acclimated mussels, determined in the cold condition, were not significantly different from zero ($P>0.05$, n=16). Calcium and potassium losses were increased in magnitude with the transfer of cold-acclimated zebra mussels to room temperature ($P<0.01$, n=16 each).

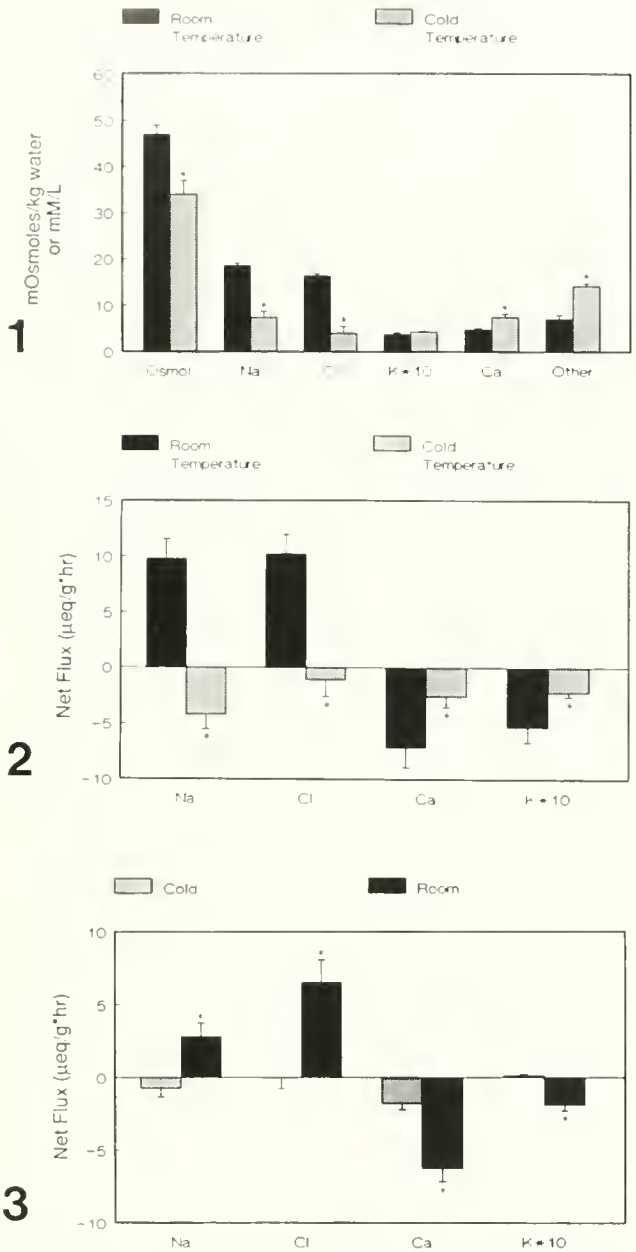
DISCUSSION

Zebra mussels in artificial pondwater maintained in laboratory conditions without being fed had hemolymph ion values close to hemolymph values of mussels collected from the field. However, mussels maintained in cold pondwater, for the same time period, lost sodium and chloride with a resulting net reduction in hemolymph osmolarity. The loss of sodium and chloride from *Dreissena polymorpha* and *Lampsilis radiata* was similar to the effect of salt depletion (Murphy & Dietz, 1976; Scheide & Dietz, 1982). Yet, the cold acclimated mussels were in a medium that had sufficient ions for mussels to maintain sodium and chloride balance at a warmer temperature.

Sodium and chloride net fluxes usually were positive in room temperature acclimated zebra mussels. However, with acute transfer of room temperature-acclimated zebra mussels to cold pondwater, mussels lost sodium and chloride. The loss of sodium and chloride, observed in the cold pondwater treatment, was reflected in the reduced hemolymph sodium and chloride concentrations observed with cold pondwater acclimation. Metabolic activity, measured as oxygen consumption, of zebra mussels is reduced with colder water temperatures (McMahon & Alexander, 1991; Quigley, Gardner & Gordon, 1993). The apparent loss of sodium and chloride observed in the room temperature-acclimated zebra mussels when transferred to cold pondwater may be related to reduced metabolic activity. However, long term acclimation of zebra mussels to cold pondwater resulted in a reduction of the net sodium and chloride loss to values close to zero. The change in ion loss attributed to zebra mussel cold storage may be the result of a decreased ionic gradient due to the animal loss of sodium and chloride or may be due to changes in epithelial ion transport and ion permeability, thus the mussels become "tighter" to the loss of ions. Cold acclimated mussels, transferred back to the room temperature pondwater exhibited a positive net flux for sodium and chloride. Thus, the ion transport mechanisms necessary for regulating sodium and chloride balance were present in the cold acclimated zebra mussels but their activity was reduced in cold pondwater.

All net ion fluxes studied varied with temperature regime. Zebra mussels not only exhibited decreased sodium and chloride net fluxes, but decreases in magnitude of calcium and potassium net fluxes. At room temperature, both calcium and potassium net fluxes were negative. The artificial pondwater used in this investigation, while fully compatible for maintaining unionid mussels (Dietz, 1985) and zebra mussel hemolymph for extended periods of time, may not be the best medium for zebra mussels. The calcium loss indicates that this bathing medium is negatively influencing calcium balance. Even with the calcium efflux, hemolymph calcium values do not change at room temperature, thus calcium is presumably being mobilized from the shell to maintain a relatively constant hemolymph calcium value.

Even with the negative net calcium flux observed in the zebra mussel, hemolymph calcium concentrations increased as the hemolymph osmolarity decreased. Hemolymph calcium also increased in the unionid, *L. radiata*, during cold pondwater conditions. The rise in hemolymph calcium concentrations in cold acclimated-mussels may be assisted by the decrease in the net calcium loss at the lower temperature. The elevation of hemolymph calcium has been noted with the decrease in hemolymph sodium in unionids (Scheide & Dietz, 1982). Only in *L. radiata* did the "other" ions increase with cold acclimation. Similar changes have been observed in the unionid, *Ligumia subrostrata* (Say) undergoing chloride depletion (Scheide & Dietz, 1982). Cold pondwater storage of mussels caused an increase in calcium levels concomitant with the decrease of sodium levels suggesting that compensatory mechanisms, al-



Figures 1–3. Comparisons of the effects of temperature on ion concentations in *Lampsilis radiata* and *Dreissena polymorpha*. **1.** Hemolymph ion concentrations of *Lampsilis radiata* after a 10 day acclimation period to room temperature (21 ± 1°C, solid bar) and cold temperature (4 ± 1 °C, hatched bar). K•10 refers to the potassium value multiplied by 10 for comparison purposes. "Other" refers to the difference between the measured total solute and sum of the measured ion values, as noted in the Materials and Methods section and indicates the hemolymph bicarbonate concentration. The capped lines indicate the standard error of the mean. Significant differences are denoted with a • representing $P < 0.05$ with n=8 for room and cold temperature-acclimated mussels. **2.** Effects of direct transfer of 21°C ± 1°C acclimated zebra mussels to 4°C on the sodium, chloride, calcium and potassium net fluxes. The potassium net flux is increased 10 fold for comparative purposes (K•10). The room temperature acclimated mussel net flux is denoted by the solid bar (n= 14 mussels for all groups except for the sodium group, n=13) and the cold net flux is denoted by the hatched bar (n=14 mussels for all groups). Significant flux differences are denoted by • ($P < 0.05$). **3.** Effects of direct transfer of 4 ± 1°C acclimated zebra mussels to 21°C on the sodium, chloride, calcium and potassium net fluxes. The potassium net flux is increased 10 fold for comparative purposes (K•10). The cold-acclimated net flux is denoted by the hatched bar (n=16 mussels) and the room temperature mussel net flux is denoted by the solid bar (n=16 mussels). Significant flux differences are denoted by • ($P < 0.05$).

though not completely effective in maintaining room temperature osmolarity, were active in the cold-acclimated mussels.

Freshwater animals have set points for hemolymph blood sodium and chloride (Kirschner, 1991). Movement of zebra mussels from the natural environment to the laboratory does not appear to negatively effect the mussels for at least 31 days. The formulation of artificial pondwater appears to be suitable for the laboratory maintenance of zebra mussels. Zebra mussels, held at room temperature, maintained hemolymph ion values close to the collection hemolymph ion values, although the mussels were in a negative calcium balance. The mussel holding time in the laboratory may be increased by placing the mussels in cold pondwater and zebra mussel storage at a cold temperature is recommended for laboratory housing of zebra mussels not immediately being used for studies (Reid, *et al*, 1993). However, the ion concentrations after holding may be depressed, particularly with a longer cold holding period and the lack of feeding. Changes in mussel physiology, due to cold storage, need to be recognized as further research is performed to understand the basic biology of the zebra mussel.

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The Muricid Types of Frank Collins Baker

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ABSTRACT

In the first ten years of his scientific career F.C. Baker named nine taxa in the family Muricidae. Of these only one, *Haustellum rubidus* (named as *Murex messorius* var. *rubidum*), is here considered valid. All others are synonyms of older names.

Key words: Muricidae, Gastropoda, F.C. Baker

INTRODUCTION

The name Frank C. Baker is very familiar to workers among land and fresh-water mollusks, but for the first ten years of his professional life he thought of himself as an expert in marine mollusks, especially the Muricidae. Of his first 21 papers, published between 1888 and 1897, only two (1895b, 1897b) are on non-marine Mollusca. His first publication (1888) was a note describing the marine mollusks collected along the coast of Massachussets.

In the "General Notes" of *The Nautilus* (3:46), it was stated that "Mr. F.C. Baker, formerly of Providence, R.I., is pursuing his studies at the Academy of Natural Sciences of Philadelphia." He spent the months of January to April, 1889, in Brevard County, Florida, and from this experience came a diverse set of notes on the marine mollusks (1889a), on the feeding habits of birds (1889b), including the identification of a number of mollusks eaten by said birds, and on the habits of the muskrat (1889c).

The first molluscan species he described was *Ocinebra jenksii* (Baker, 1889d) and in 1890 when the American Association of Conchologists was initially announced (*The Nautilus*, 3:140–143), among the charter members listed was "F.C. Baker, Academy Natural Sciences, Philadelphia, *Muricidae*." His second taxonomic paper (Baker, 1890a) was also on a muricid, with the redescription of *Urosalpinx perrugatus* (Conrad, 1846).

Among his most important contributions to the body of molluscan knowledge are his series of seminal papers on the protoconchs of the Muricidae (Baker, 1890b, 1891d, 1894) and other marine gastropods (Baker, 1897c), together with several catalogues of the species of Muricidae (Baker, 1891e, 1895c, 1897a).

In 1894 he moved to Chicago to become the first curator of mollusks at the newly constructed Academy of Sciences (see Baker, 1895a), a position he held for the next 20 years (Franzen, 1958:30), and it is only then that his interests turned to non-marine mollusks, beginning with an important paper (1895b) on the transport of land and fresh-water mollusks by means of birds, fish, etc. (possibly the first report of "ducks with dirty feet" transporting embryonic shells). Although he published three more papers (1895c, 1897a, 1897c) on marine mollusks, after 1898 he never again digressed from non-marine faunas.

In the time that he was studying muricids Baker described nine new taxa, only four of which (those in the 1891d work) were figured. For the most part these species have been ignored by subsequent workers. Keen (1971: 554) noted that *Ricinula rugosoplicata* Baker is a synonym of *Buccinum lugubre* C.B. Adams, 1852, and Vokes (1971) attempted to assign the species to generic taxa, with varying degrees of success (see below). Radwin and D'Attilio (1976) did nothing with the species, except to list two as "species of uncertain identity" (*bituberculatus* and *jenksi* [*sic*], p. 217). Only two taxa named as "varieties" have ever been the subject of any discussion: *Murex haustellum* var. *longicaudus* and *Murex messorius* var. *rubidum*.

In a monograph on the Indo-Pacific species of *Chicoreus* Houart (1992, fig. 371) refigured the holotype of *Murex (Chicoreus) bituberculatus*, from the collection of the Chicago Academy of Sciences. This, combined with an on-going study on the species of Ergalataxinae, to which I suspected certain of Baker's species might belong, caused me to contact Mr. Ron Vasile, Curator of Mollusks at the Chicago Academy, and through him I arranged to borrow the type material of these little known taxa. To complete the study I also contacted the Academy of Natural Sciences of Philadelphia, where four additional types were located, and the Wagner Free Institute of Science, Philadelphia, which supposedly had one type lot that could not be located.

Because these taxa are so poorly known, it seems worthwhile to present all of them in one place, and they are listed below in chronological order as originally described. Unfortunately, most prove to be synonyms of previously described species. Even though this is not a

"revisionary work," because there are multiple specimens of certain of the taxa, it seems advisible to designate lectotypes. It is unlikely that most of the taxa will ever be treated in any strictly monographic work.

SYSTEMATICS

Ocinebra jenksii
Figures 1, 2

Ocinebra jenksii Baker, 1889d:80
?*Urosalpinx jenksii* (Baker). Vokes 122

Habitat: Unknown.

Lectotype: ANSP 36099 (here designated) (fig. 1).

Paralectotypes: CAS 20696[1] (fig. 2); ?WFIS (not found).

Discussion: Baker compared *O. jenksii* to the Californian species *Ocenebra circumtexta* Stearns, 1872, *O. gracillima* Stearns, 1872, and *O. michaeli* Ford, 1888, suggesting that he perhaps thought it might also be from California. However, examination of the two extant type specimens indicates that it is an elongate form of the variable common southern Australian *Lepsiella vinosa* (Lamarck, 1822) (see fig. 3).

In the original description, Baker (1889d:81) noted that there were four specimens "obtained from the Wagner Collection at the Wagner Free Institute of Science." A search of the collections of the Institute did not uncover any specimens but at the Academy of Natural Sciences of Philadelphia, where Baker worked at the time, there is a specimen (ANSP 36099; height 16.5 mm, diameter 9.5 mm) labeled as "syntype" that nearly matches the cited dimensions ("Alt. 17, diam. 10 mm"). This specimen is designated as the lectotype. There is one paralectotype (CAS 20696) in the collections of the Chicago Academy of Sciences, which is slightly smaller (height 15.1 mm, diameter 8.3 mm). The fate of the two additional paralectotypes is not known.

Murex haustellum Linné var. *longicaudus*
Figure 4

Murex haustellum Linné var. *longicaudus* Baker, 1891b:56
Haustellum longicaudus (Baker). Vokes, 1971:66
Not *Haustellum longicaudum* [*sic*] (Baker). Kaicher, 1973, 2:124 (= *H. kurodai*).
Not *Haustellum longicaudus* (Baker). Fair, 1976:55, fig. 50 (= *H. kurodai*)
Haustellum haustellum haustellum (Linné) Ponder and Vokes, 1988:86, figs. 46C, 46D ("holotype" [lectotype] of *H. longicaudus*)
Haustellum haustellum longicaudus (Baker). Houart, 1990:332, figs. 12, 13, 29

Habitat: Red Sea

Lectotype: ANSP 60965 (here designated).

Paralectotype: CAS 20701 (fig. 4).

Discussion: Most authors (*e.g.*, Radwin & D'Attilio, 1976:49, Ponder & Vokes, 1988:86) have considered this "variety" to be a synonym of typical *Murex haustellum*. However, Houart (1990:332) has expressed the opinion that the differences in the nature of the protoconch between *Haustellum haustellum* s.s. (see Ponder & Vokes, 1988, fig. 78D, Houart, 1990, fig. 31) and forms from the Indian Ocean named *longicaudus* (see Houart, 1990, fig. 29) and *Haustellum* sp. (Houart, 1990, fig. 32) indicate three distinct species. Given that all three have protoconchs of 2 to 2.5 whorls and the major difference is in the whorl shape, ranging from rather conical in the typical Indo-West Pacific form, to cylindrical in the East African form (*Haustellum* sp.), to somewhat bulbous in the Red Sea form (*longicaudus*), his argument is not especially compelling.

The differences in teleoconch morphology are less between these three forms than between the typical *H. haustellum* s.s. and populations named as *H. kurodai* (Shikama, 1964) and *H. vicdani* Kosuge, 1980 (see Ponder & Vokes, 1988, figs. 87A-C: *kurodai*, *vicdani*, and *haustellum* s.s., respectively), thus it is probable that the Indian Ocean, Red Sea populations represent only morphological variation as well.

In the original description Baker (1891b:56) stated that he had three specimens of this variety, one of which was in the collections of the Academy of Natural Sciences of Philadelphia and "two are in my collection." The specimen in the collections of the Philadelphia Academy (ANSP 60965) is here designated as the lectotype and the one (fig. 4) in the Chicago Academy of Sciences (CAS 20701) is a paralectotype. I do not know where the third specimen is today.

Ocinebra pilsbryana
Figures 5–7

Ocinebra Pilsbryana Baker, 1891b:57
?*Urosalpinx pilsbryana* (Baker). Vokes, 1971:125

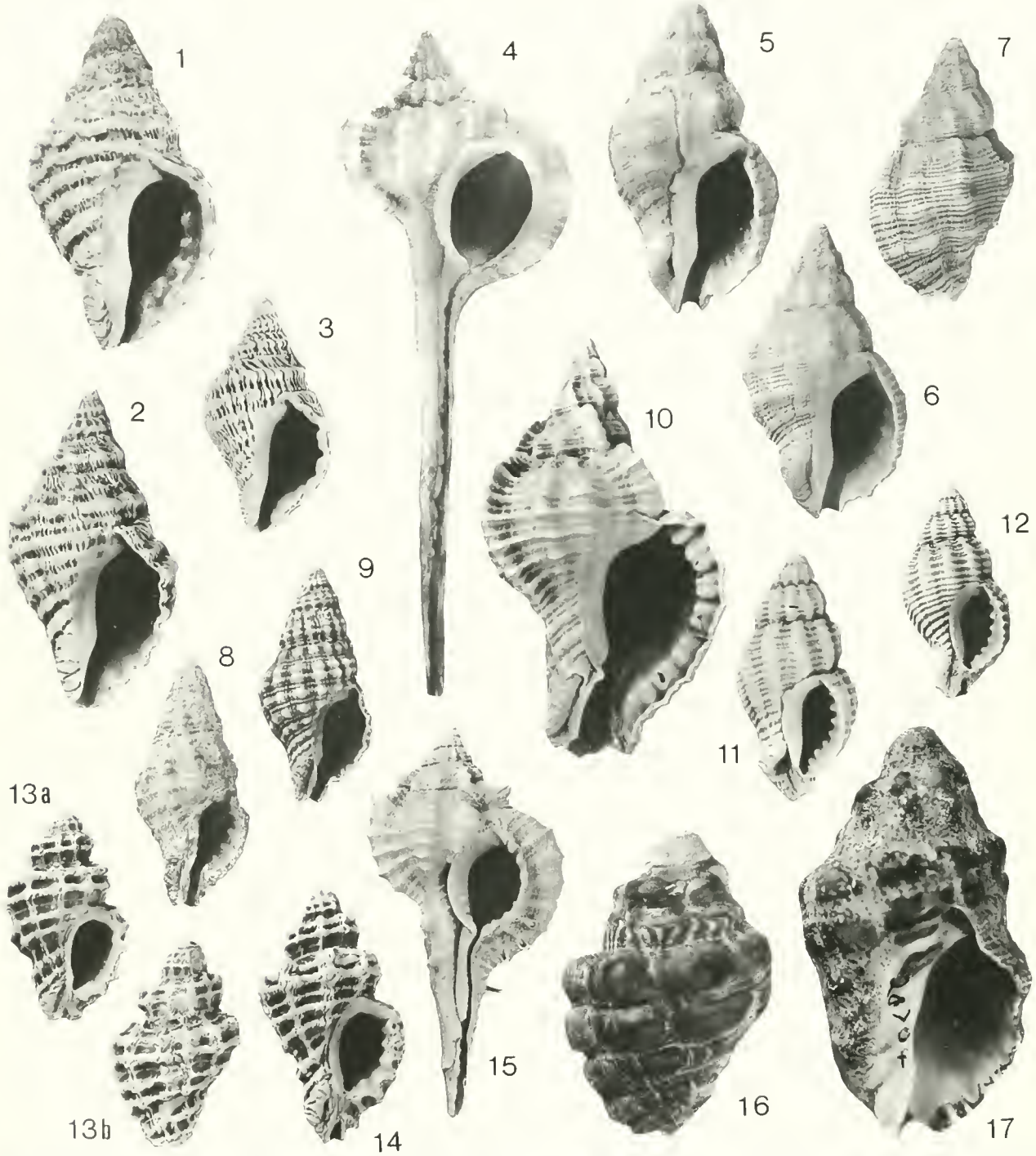
Habitat: Ceylon.

Lectotype: ANSP 60307 (here designated) (fig. 5).

Paralectotypes: CAS 20699A and 20699B (figs. 6, 7).

Discussion: Baker stated that this species "has features recalling the genera *Trophon*, *Urosalpinx*, and *Sistrum*" (1891b:58) and he is not the only person who has had difficulty placing it. Examination of the type specimens (figs. 5–7) shows it to be a subjective synonym of *Ergalatax contracta* (Reeve, 1846), which also has been attributed to several different genera by other authors: *Buccinum contractum* Reeve, 1846; *Murex calcareus* Dunker, 1860; *Urosalpinx innotabilis* E.A. Smith, 1879; *Pentadactylus ceylonicum* Preston, 1909; and *Morula martensii* Dall, 1923.

[1] Both the Chicago Academy of Sciences and the California Academy of Sciences use the abbreviation "CAS" for specimen identification. In every case in this paper the reference CAS is to the Chicago Academy of Sciences.



Figures 1–2. *Ocinebra jenksii* Baker. **1.** ANSP 36099 (lectotype), height 16.5 mm, locality unknown (X 3). **2.** CAS 20696 (paralectotype); height 15.1 mm, locality unknown (X 3). **3.** *Lepsiella vinosa* (Lamarck), TAM C 167197, height 8.2 mm, Recherche Bay, Tasmania, Australia (X 4). **4.** *Murex haustellum* var. *longicaudus* Baker, CAS 20701 (paralectotype); height 49.7 mm, Red Sea (X 2). **5–7.** *Ocinebra pilsbryana* Baker. **5.** ANSP 60307 (lectotype); height 15.5 mm, Ceylon (X 3). **6.** CAS 20699 (paralectotype A), height 16.0 mm, Ceylon (X 3). **7.** CAS 20699 (paralectotype B); height 14.1 mm, Ceylon (X 3). **8. 9.** *Ricinula* (*Sistrum*) *rugosoplicata* Baker. **8.** ANSP 61306 (lectotype); height 11.7 mm, Turtle Bay, Lower California (X 3). **9.** CAS 20703 (paralectotype); height 11.0 mm, Turtle Bay, Lower California (X 3). **10.** *Murex* (*Chicoreus*) *bituberculatus* Baker, CAS 20702 (holotype); height 31.7 mm, Australia (X 2). **11.** *Ocinebra wardiana* Baker, CAS 20698 (holotype); height 12.5 mm, "Australia" (X 3). **12.** *Ocinebrina aciculata* (Lamarck), Vokes Coll., height 10.6 mm, off Bota, Spain (X 3). **13.** *Ocinebra rubra* Baker, CAS 20697 (holotype); height 10.7 mm, locality unknown (X 3). **14.** *Ocenebra clathrata* (Dall), Vokes Coll.; height 10.0 mm, off Hollester Ranch, California, 15 m (X 3). **15.** *Murex messorius* var. *rubidum* Baker, USNM 878003, height 30.5 mm, Anna Maria Key, Florida, 46 m (X 2). **16. 17.** *Purpura* (*Thalessa*) *problematica* Baker. **16.** CAS 20704A (lectotype); height 30.9 mm, Japan (X 2). **17.** CAS 20704B (paralectotype); height 22.8 mm, Japan (X 2).

Often cited as a another synonym is *Ergalatax recurrens* Iredale, 1931, named as type of the genus (and hence *contracta* is usually cited as the type species of *Ergalatax*); however, *E. recurrens* is not the same as *E. contracta* but is a synonym of *Murex pauper* Watson, 1883, which is thus the correct name for the type of the genus *Ergalatax* Iredale, 1931.

There was no comment on the number of specimens in the original type lot. There is one specimen (fig. 5) in the collections of the Academy of Natural Sciences of Philadelphia (ANSP 60307), which is here designated as the lectotype; two additional specimens (figs. 6, 7) at the Chicago Academy of Sciences (CAS 20699) are designated as paralectotypes.

Ricinula (Sistrum) rugosoplicata
Figures 8, 9

Ricinula (Sistrum) rugosoplicata Baker, 1891b:58

Habitat: Turtle Bay, Lower California.

Lectotype: ANSP 61306 (here designated) (fig. 8).

Paralectotype: CAS 20703 (fig. 9).

Discussion: Keen (1971:554) included *R. rugosoplicata* in the synonymy of *Buccinum lugubre* C.B. Adams, 1852, now placed in the Ocenebrine genus *Trachypollia* and not *Morula* (*Morunella*), as Keen reported. There are two specimens in the type lot, one at the Academy of Natural Sciences of Philadelphia (fig. 8) and one at the Chicago Academy of Sciences (fig. 9). Baker (1891b:58) says "this pretty little shell was found in a collection recently purchased by the Conchological Section of the Academy of Natural Sciences from Mr. Henry Hemphill"; therefore, the Philadelphia specimen (ANSP 61306) is here designated as the lectotype.

Murex (Chicoreus) bituberculatus
Figure 10

Murex (Chicoreus) bituberculatus Baker, 1891d:133, pl. 11, fig. 4
Chicoreus bituberculatus (Baker). Vokes, 1971:24
Murex bituberculatus Baker. Fair, 1976:26; Houart, 1992:106, fig. 371 (holotype)

Habitat: Australia.

Holotype: CAS 20702 (fig. 10).

Discussion: Fair (1976:26) was the first to suggest that *M. bituberculatus* is a juvenile specimen of *Chicoreus capucinus* (Lamarck, 1822). Examination of the holotype shows that she was correct. Although the locality "Australia" at first seems misleading, *C. capucinus* does occur in the tropical mangrove areas of northern Australia.

Ocinebra wardiana
Figure 11

Ocinebra wardiana Baker, 1891d:134, pl. 11, fig. 5.
Ocinebrina wardiana (Baker). Vokes, 1971:127; Fair, 1976:86, fig. 65 (after Baker)

Habitat: "Australia."

Holotype: CAS 20698 (fig. 11).

Discussion: Evidently the erroneous locality of "Australia" convinced Baker (1891d:134) that this species, although "having a superficial resemblance to *Ocinebra aciculata* Lam.," was to be distinguished by its larger size, more developed umbilical region, and its yellow color, differing from the "light rosy" Mediterranean species *Ocinebrina aciculata* (Lamarck, 1822). True, this gerontic example is larger than most specimens of *O. aciculata* but Radwin and D'Attilio (1976:125) cite 16 mm as maximum height for this species; they also note that the color ranges from orange-brown to red-brown to purple-brown. Comparison of the type of *O. wardiana* to a typical Mediterranean example of *O. aciculata* (fig. 12) fails to show any significant differences. Nothing like it has ever been recognized from Australian waters.

Ocinebra rubra
Figure 13

Ocinebra rubra Baker, 1891d:134, pl. 11, figs. 6, 7
Ocinebrina rubra (Baker). Vokes, 1971:126; Fair, 1976:73, fig. 52 (after Baker).

Habitat: Unknown.

Holotype: CAS 20697 (fig. 13).

Discussion: Although compared by Baker to *Favartia alveata* (Kiener, 1842) and *F. peasei* (Tryon, 1880), the only resemblance is the development of deep pits formed by the intersection of the axial and spiral ribs. Baker (1891d:135) further noted "it has some resemblances to the figures of *Ocinebra interfossa* Cpr." and here he is much closer to the truth. In fact, the same form (see fig. 14) was later named *Tritonalia interfossa* var. *clathrata* by Dall (1919:324; holotype figured by Bormann, 1946, pl. 4, fig. 2; Fair, 1976, fig. 315; Kaicher, 1978, no. 1615).

If one considers this a valid species, then Baker's name is the correct one to use. Most workers, however, consider the form to be a synonym of *Ocenebra atropurpurea* Carpenter, 1865 (lectotype figured by Bormann, 1946, pl. 4, fig. 8; Palmer, 1958, pl. 23, figs. 2, 3, 13; Fair, 1976, fig. 316; Kaicher, 1978, no. 1627), which originally was named as a variety of the common California species *O. interfossa* Carpenter, 1864 (holotype figured by Bormann, 1946, pl. 4, fig. 10; Palmer, 1958, pl. 23, fig. 1; Fair, 1976, fig. 318; Kaicher, 1978, no. 1614). *Ocenebra rubra/clathrata* is no more than a shouldered form of *O. atropurpurea*, and both are simply clathrate varieties of the *O. interfossa* complex.

Purpura (Thalessa) problematica
Figures 16, 17

Purpura (Thalessa) problematica Baker, 1891d:135, pl. 11, figs. 2, 3

Habitat: Japan [Seta coast, Japan, *fide* Franzen, 1958:34, from label with specimens].

Lectotype: CAS 20704A (designated by Franzen, 1958: 34) (fig. 17).

Paralectotype: CAS 20704B (fig. 16).

Discussion: Inasmuch as *P. problematica* is unquestionably a synonym of the common Japanese species *Purpura clavigera* Kuster, 1860, one can only assume that Baker was misled by Tryon (1880:163), who dismissed *P. clavigera* as "a depauperate form" of *P. tumulosa* Reeve, 1846, the species to which Baker compared *problematica*. Baker (1891d:136) further added that "this species is well figured on pl. 46, f. 48 of the second volume of Tryon's Manual," which is a reproduction of the shell Lischke (1869, pl. 5, fig. 15) figured as *P. tumulosa* Reeve. The latter is not Reeve's species but the nodulose form of *P. clavigera*, as Lischke demonstrates in his series of illustrations (1869, pl. 5, figs. 12–16). Both morphotypes have been well figured by Kaicher (1980, no. 2481).

Reeve's species *P. tumulosa* is a synonym of *Thais* (*Tenguella*) *marginalba* (Blainville, 1832), a widespread Indo-Pacific species that does occur in eastern Africa, and Reeve's locality of "Zanzibar" is probably not erroneus, as suggested by Tryon. Members of the *P. clavigera* complex have been placed in the subgenus *Thais* (*Reishia*) Kuroda and Habe, 1971, type species: *Purpura bronni* Dunker, 1860.

There were said to be 12 specimens in the type lot, two of which were figured in the original description. Franzen (1958:34) selected the larger of these (Baker, 1891d, pl. 11, fig. 3) as the lectotype. Both specimens are figured here (figs. 16, 17).

Murex messorius var. *rubidum*
Figure 15

Murex messorius var. *rubidum* Baker, 1891d:137 (nude name, list only); 1897a:377
Murex (*Murex*) *recurvirostris rubidus* Baker. Clench and Pérez Farfante, 1945:6, pl. 3, figs. 1–7 (figs. 1, 2 lectotype).
Murex (*Murex*) *rubidus* Baker. Vokes, 1963:108, pl. 4, figs. 3, 4.
Murex rubidus Baker. Vokes, 1971:92, Radwin and D'Attilio, 1976:71, pl. 11, fig. 45; Fair, 1976:73, fig. 40
Haustellum rubidus (Baker). Vokes, 1990:17, pl. 1, fig. 12
Murex rubidus panamicus Petuch, 1990:62, fig. 8

Habitat: Cedar Keys, Florida.

Lectotype: Harvard MCZ 147272 (designated by Clench and Pérez Farfante, 1945:8).

Discussion: This is the most widely recognized of Baker's taxa, and was only inadvertantly named by Baker, who credited the varietal name to Dall (1889:196). In that reference Dall describes the Florida specimens of *Murex messorius* as "often of a deep rose-color . . . less hooked and spinose than the discolored specimen figured by Reeve [1845, pl. 22, fig. 90, which is a good example of typical *messorius*]." However, nowhere does Dall mention the word "*rubidum*" and the name must date to Baker's 1897 usage, where he does give a description of sorts ("the shell being of a deep-pink color," 1897a:377), which together with the Florida locality is sufficient to identify the species.

Clench and Pérez Farfante (1945:8) recognized the Florida form as a valid subspecies of the Pacific *recurvirostris* Broderip, 1833, changing "*rubidum*" to the orthographically correct *rubidus*, and noting that the species is not only pink but comes in "cream, pink, pale orange, salmon, or even red" and some specimens possess darker color bands at the shoulder and base of the body whorl.

Although generally confined to the Florida and Bahamian areas, specimens also occur in the Bay Islands of Honduras, the northern coast of South America, and Panama (see Vokes, 1990:17). The latter have been separated as a geographic subspecies by Petuch (1990:62, fig. 8).

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ABBREVIATIONS OF REPOSITORY COLLECTIONS

ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
CAS – Chicago Academy of Sciences, Chicago, Illinois, USA
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachussets, USA
TAM – The Australian Museum, Sydney, New South Wales, Australia
USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
WFIS – Wagner Free Institute of Science, Philadelphia, Pennsylvania, USA

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Invasion of the Rivers of the Littoral Central Region of Venezuela by *Thiara granifera* and *Melanoides tuberculata* (Mollusca: Prosobranchia: Thiaridae) and the Absence of *Biomphalaria glabrata*, Snail Host of *Schistosoma mansoni*

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ABSTRACT

Prior to 1975, some streams of the littoral central region of Venezuela were active transmission sites for intestinal schistosomiasis. The snail intermediate host, *Biomphalaria glabrata*, was controlled but not eliminated by repeated molluscicide applications. Two thiarid snails, *Thiara granifera* and *Melanoides tuberculata*, began to invade these streams around 1975. The rapid expansion of these two species was confirmed during more recent surveys. Although other factors may be involved, the existence of stable populations of the two thiarid species is probably linked to the absence of recolonization by *B. glabrata*, the latter species has not been observed in the study region during the last 15 years.

Key words: Schistosomiasis, thiarid, recolonization

INTRODUCTION

The littoral central region of Venezuela forms the northern portion of an endemic area for intestinal schistosomiasis. Some of the rivers of this region have previously offered, and may still constitute, suitable habitats for the snail intermediate host, *Biomphalaria glabrata* (Say, 1818); they may thus act as potential transmission sites for the parasite (Incani, 1987). A control program, based on chemotherapy, sanitation, health education, environmental improvements and applications of molluscicides was initiated in 1943. This control program resulted in the near total interruption of transmission of *Schistosoma mansoni* (Sambon, 1907) during the 1970's (Incani, 1987). Several malacological surveys carried out in the lower course of the rivers before 1975 had revealed the presence of *B. glabrata*. More recent surveys, undertaken between 1975 and 1983, and in 1990, demonstrated the

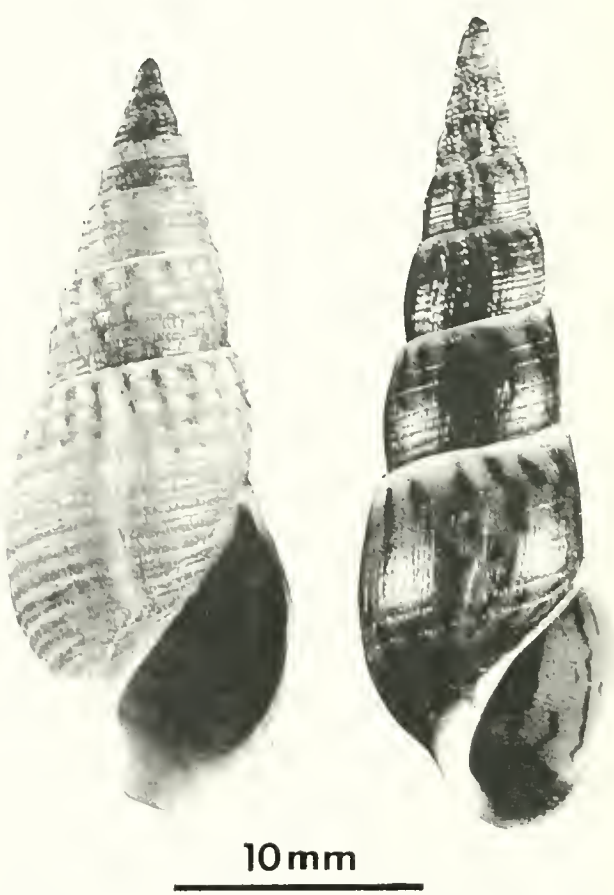


Figure 1. *Thiara granifera* (left) and *Melanoides tuberculata* (right).

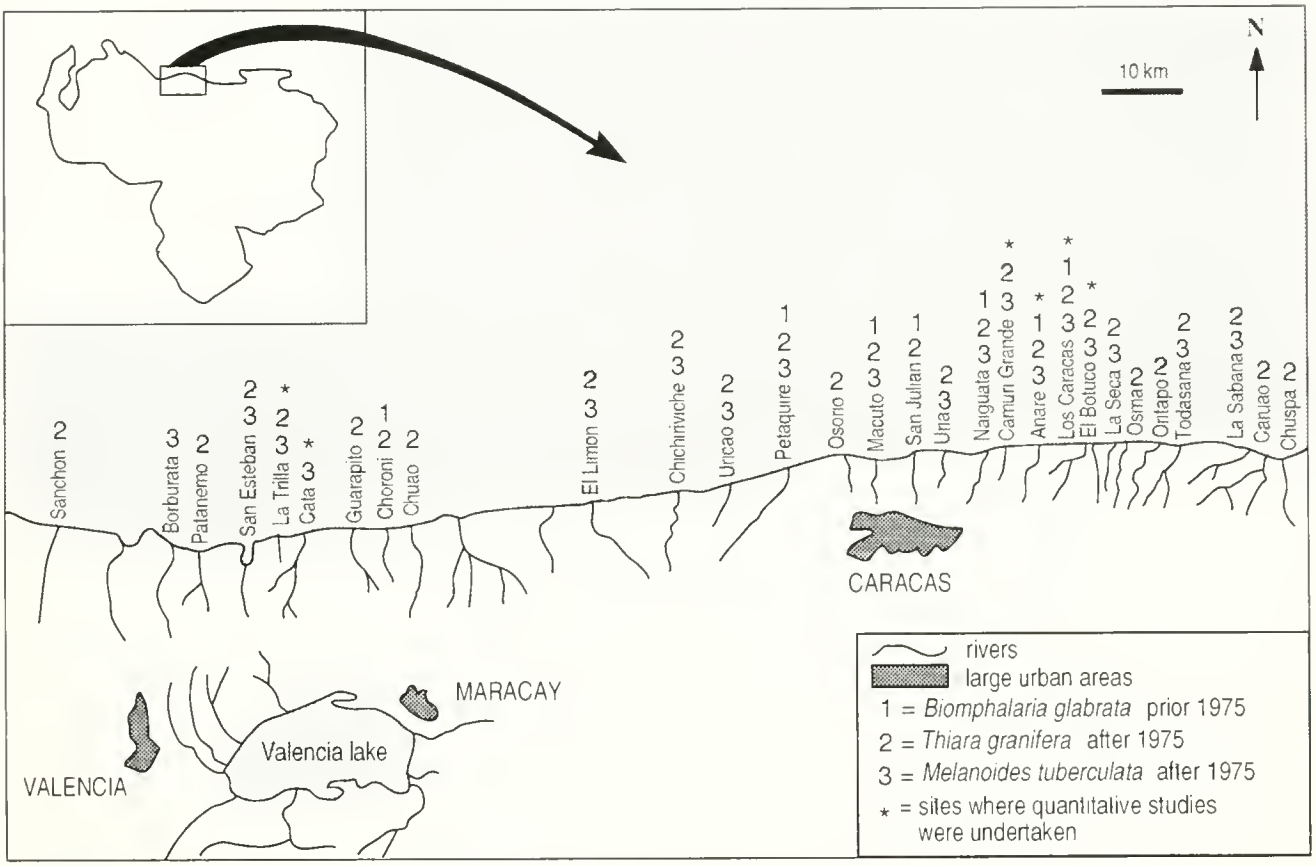


Figure 2. Map of the littoral central region of Venezuela showing the surveyed rivers

invasion of these rivers by two species of Thiaridae, *Thiara granifera* (Lamarck, 1822) and *Melanoides tuberculata* (Müller, 1774)(Figs. 1, 2).

Thiara granifera was introduced to the Caribbean area around 1935 (Murray & Woopschal, 1965) and to Venezuela in 1970 (Chrosciechowski, 1973). It was first observed in the littoral central region in 1975. The introduction of *M. tuberculata* to the Caribbean area probably occurred later. It was reported for the first time in Texas in 1964, but according to Murray (1964), it probably was introduced there several years earlier. *M. tuberculata* appeared in Venezuela in 1972 (Chrosciechowski, 1973), and its presence in the rivers of the littoral, central region coincided with that of *T. granifera*. This paper presents the results of malacological surveys carried out in all these rivers between 1975 and 1983, and in 1990.

METHODS

Twenty-nine rivers were sampled along the littoral central region of Venezuela (Fig. 2). All are permanent, short and rocky streams descending rapidly from the mountains of the littoral cordillera; the upper stretches constitute the typical habitat of the local thiarid snail *Pachychilus laevissisimus* (Sowerby, 1824). The lower courses, often polluted in urbanized areas, provide suitable habitats for the snail *B. glabrata*. Only the lower parts of the rivers were investigated during this study.

Qualitative data were collected on the presence or apparent absence of the main species of snails before 1975, between 1975 and 1983, and in 1990 during the control program monitored by the Ministry of Health (Chrosciechowski *et al.*, 1987; Balzan, 1988). Samplings using a quadrat method were carried out in six sites located on the lower courses of the Cata, La Trilla, Camuri Grande, Anare, Los Caracas and El Botuco Rivers in 1990. All snails were manually collected and counted in squares of 0.1 m^2 regularly spaced at one meter intervals along four or five transects crossing the river.

RESULTS

Prior to 1975, seven of these rivers harbored *B. glabrata* (Fig. 2 and Table 1) and were also active transmission sites for schistosomiasis. These rivers were treated several times with molluscicides (sodium pentachlorophenate) during the 1960's (Alarcon de Noya *et al.*, 1987).

In 1975, *T. granifera* and *M. tuberculata* were first discovered in the Naiguata, Anare and Los Caracas Rivers, and in other rivers in subsequent years. General surveys, carried out between 1975 and 1983, showed that these two species had become dominant in many rivers (Table 1). In 1990, another survey demonstrated the in-

Table 1. Malacological observations made in twenty rivers of the littoral central region of Venezuela *B.g. Biomphalaria glabrata*; *T.g. Thiara granifera*, *M.t. Melanoides tuberculata*, *P.l. Pachychilus laevississimus*.

Rivers	Snail fauna			Molluscicide application (last year)
	< 1975	1975–1983	1990	
Sanchon	—	—	*T.g.*	—
Borburata	—	—	*M.t.*	—
Patanemo	—	—	*T.g.*	—
San Esteban	—	—	*T.g./M.t.*	—
La Trilla	—	—	*T.g./M.t./P.l.*	—
Cata	—	—	*M.t.*	—
Guarapito	—	—	*T.g.*	—
Choroni	*B.g.*	—	*T.g.*	—
Chuao	—	—	*T.g.*	—
El Limon	—	*T.g./M.t.* (1983)	*T.g./M.t./P.l.*	—
Chichiriviche	—	*T.g./M.t.* (1980)	*T.g./M.t.*	—
Uricao	—	*T.g./M.t.* (1977)	—	—
Petaquire	*B.g.*	*T.g./M.t.* (1977)	—	1967
Osorio	—	*T.g.* (1983)	—	—
Maouto	*B.g.*	*T.g./M.t.* (1976)	*T.g./M.t.*	1962
San Julian	*B.g.*	*T.g.* (1984)	*T.g.*	1984
Uria	—	*T.g./M.t.* (1980)	—	—
Naiguata	*B.g.*	*T.g./M.t.* (1975)	*T.g./M.t.*	1962
Camuri Grande	—	*T.g./M.t.* (1979)	*T.g./M.t./P.l.*	—
Anare	*B.g.*	*T.g./M.t.* (1975)	*T.g./M.t.*	1963
Los Caracas	*B.g.*	*T.g./M.t.* (1975)	*T.g./M.t.*	1965
El Botuco	—	*T.g.* (1979)	*T.g./M.t.*	—
La Seca	—	*T.g./M.t.* (1978)	—	—
Osma	—	*T.g./M.t.* (1979)	*T.g.*	—
Oritapo	—	*T.g./M.t.* (1979)	*T.g.*	—
Todasana	—	*T.g./M.t.* (1979)	*T.g./M.t.*	—
La Sabana	—	*T.g.* (1979)	*T.g./M.t.*	—
Caruao	—	*T.g.* (1979)	—	—
Chuspa	—	*T.g.* (1979)	*T.g.*	—

vasion of most of the rivers of this region by the two thiarids and confirmed the absence of *B. glabrata* (Table 1).

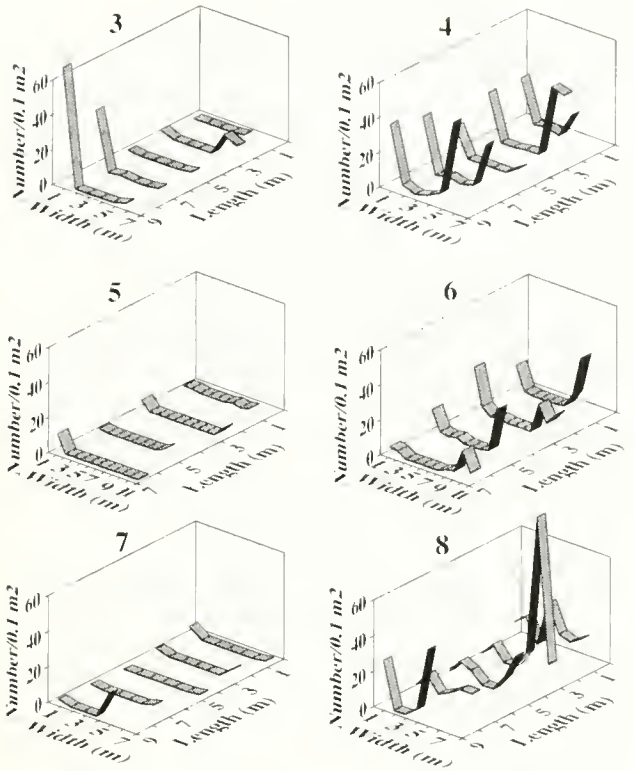
Sampling carried out in 1990 by the quadrat method determined the spatial colonization and densities of snails in these six rivers. The two species of Thiaridae mainly colonized the edges or protected areas in five of the six sites (Figs. 3–14). These sites, with one exception, were characterized by a strong current throughout the year and the variable presence of rocks, stones, gravel and sand. Snail densities were not uniform, but showed an aggregated distribution. In this ecological situation *T. granifera* was often more dense than *M. tuberculata*. The observed maximum densities expressed as snails per 0.1 m^2 were of 50 *T. granifera* and 67 *M. tuberculata* for the Cata River; 31 *T. granifera* and 10 *M. tuberculata* for the La Trilla River; 90 *T. granifera* and 15 *M. tuberculata* for the Camuri Grande River; 23 *T. granifera* and 5 *M. tuberculata* for the Anare River; and 46 *T. granifera* and 9 *T. tuberculata* for the Los Caracas River (Figs. 3–14).

The sixth site, located on the El Botuco River, was ecologically distinct and characterized by a sandy bottom and very low velocities. Snail densities were low; *T. granifera* reached a maximum density of 10 individuals per 0.1 m^2 and occupied mainly the center of the river, whereas *M. tuberculata* occurred at the edges at densities as high as 9 individuals per 0.1 m^2 (Figs. 13–14).

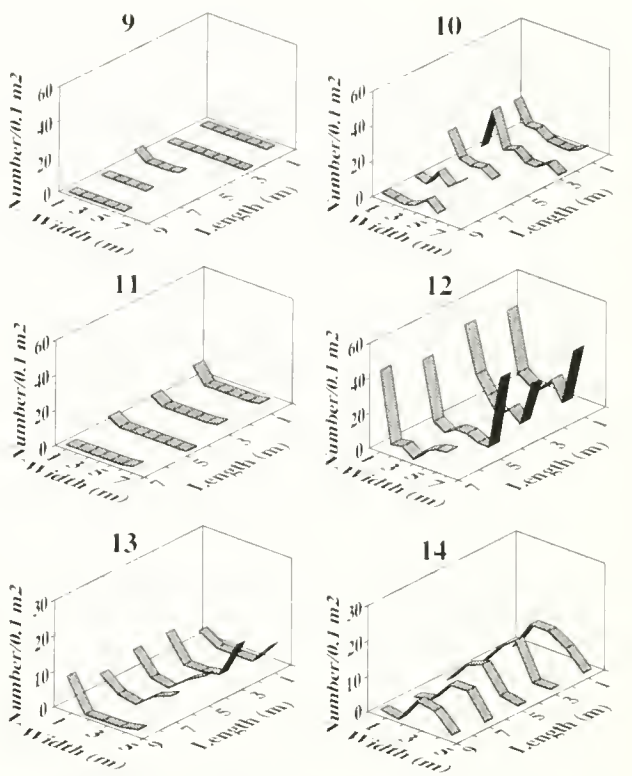
DISCUSSION

Several biological control programs using *M. tuberculata* as a competitor of *Biomphalaria spp*, were initiated in the Caribbean area (Prentice, 1983; Pointier, 1989; Pointier *et al.*, 1989). In four field trials on St. Lucia, *B. glabrata* was apparently eliminated from permanent marshes and streams, 6 to 22 months after the introduction of the competitor (Prentice, 1983). In Martinique, *M. tuberculata* was introduced to groups of water-cress beds and eliminated or strongly reduced densities of the snail hosts, *B. glabrata* and *B. straminea*, in less than two years (Pointier *et al.*, in press). In Venezuela, the introduction of thiarid snails to different types of habitats in the Valencia lake region (Fig. 2) resulted in the elimination of *Biomphalaria spp.* from three artificial ponds. However, results were negative in several streams and rivers (Pointier *et al.*, 1991).

The rivers of the littoral central region are very short and rocky, descending rapidly from the cordillera; the water velocities are often high. The thiarid snails mainly



Figures 3–8. Snail densities per 0.1 m² in three rivers of the littoral central region of Venezuela **3.** Cata River, *Melanoides tuberculata* **4.** Cata River, *Thiara granifera* **5.** La Trilla River, *M. tuberculata* **6.** La Trilla River, *T. granifera* **7.** Camuri Grande River, *M. tuberculata*. **8.** Camuri Grande River, *T. granifera*



Figures 9–14. Snail densities per 0.1 m² in three rivers of the littoral central region of Venezuela **9.** Anare River, *Melanoides tuberculata* **10.** Anare River, *Thiara granifera* **11.** Los Caracas River, *M. tuberculata* **12.** Los Caracas River, *T. granifera* **13.** El Botuco River, *M. tuberculata* **14.** El Botuco River, *T. granifera*

occupy the edges and other protected areas (Figs. 3, 4). Rocks and stones play an important role offering many refuges against the strong current and flooding. The rivers of the Valencia lake basin are ecologically different, with substrates mainly of gravel and sand. Consequently, these latter rivers offer few suitable habitats for *T. granifera* or especially for *M. tuberculata* (Pointier *et al.*, 1991). The importance of water velocity as a limiting factor for freshwater pulmonate populations has been described by several authors. Scorza *et al.*, (1961) found a negative linear correlation between water velocities and densities of *B. glabrata* in Venezuelan streams. In Puerto Rico, *B. glabrata* populations did not survive in portions of streams steeper than 20 meters per 1000 meters of length (Harry and Cumbie, 1956). Jobin and Ippen (1964) investigated the behavior of *B. glabrata* in irrigation canals and found that snails were dislodged when the flow rate exceeded 65 cm/s. More recently, Dussart (1987) studied the effects of water flow on the detachment of several species of pulmonate snails and found significant differences between species. The resistance of thiarid snails to the current is not known, but the distribution patterns of the different species in the rivers of littoral central region of Venezuela indicate that *T. granifera* is better adapted than *M. tuberculata*. Experimental studies remain to be undertaken.

It is reasonably well established that *T. granifera* and *M. tuberculata* began to invade the rivers of this region around 1975. Before 1975 several streams were active transmission sites for schistosomiasis and repeated molluscicide applications allowed good control of the snail host. However, in 1980, *B. glabrata* was again found in the San Julian River and was responsible for the reappearance of an important focus of *S. mansoni* (Alarcon de Noya, 1987). Several molluscicide treatments between 1980 and 1984 destroyed the *B. glabrata* colonies. Some months after the last treatment, an important colonization by *T. granifera* was noted. During the following years, dense and stable populations of the thiarid snail were established, and *B. glabrata* never reappeared. In Puerto-Rico, a study of the distribution of freshwater snails in a small stream showed that within five years, *T. granifera* had displaced *B. glabrata* from the central portion of the stream, suggesting some form of competition (Butlers *et al.*, 1980). Therefore, it seems probable that the colonization of the San Julian River by dense populations of the thiarid snail is now playing a major role in preventing the reappearance of the snail hosts.

The colonization of the rivers by the two species of Thiaridae appears particularly efficient. When the current is strong, *T. granifera* outnumbers *M. tuberculata*, and the two snails are confined to the banks of the streams

and to the protected areas. When the current is weak, all the river bed is colonized, but *T. granifera* occupies the central portion of the habitat while *M. tuberculata* occurs at the edges.

The last malacological survey, carried out in 1990 in the lower course of twenty three rivers demonstrated the total dominance of the two thiarid species. However, a few *N. punctulata* and *P. laevississimus* were collected in the Oritapo, Camuri Grande and Limon Rivers. The current presence of stable and dense populations of the two thiarids in nearly all the rivers of this region probably constitutes an important deterrent to the reappearance of *B. glabrata*, although other factors may be involved.

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Corbicula and *Neocorbicula* (Bivalvia: Corbiculidae) in the Paraná, Uruguay, and Río de La Plata Basins

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ABSTRACT

Corbicula Megerle, 1811 is represented in Argentinean waters by *Corbicula fluminea* (Müller, 1774) and *Corbicula largillierti* (Philippi, 1844). The distribution of *Corbicula* in the Paraná, Uruguay and Río de La Plata basins is reviewed based on published reports and collections at the Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales (MACN). Since its introduction about two decades ago, *Corbicula* has spread rapidly along the littoral regions of the Río de La Plata to Punto Indio on the western shore, and arroyo Cufré (San José Department) on the eastern shore. The genus has recently been reported to occur in the Uruguay River from Gualeguaychú to Río de La Plata. Additional records from the Paraná River at Paso de La Patria, Isla Barranqueras and Bella Vista are reported. In order to clarify the status and taxonomy of the corbiculids of the area, a brief comparative analysis of the morphology of *Corbicula* and *Neocorbicula* Fischer, 1887, is provided.

Key words: *Corbicula*, *Neocorbicula*, Argentina, distribution, introduced species.

INTRODUCTION

The family Corbiculidae is represented in the southern neotropical region by the native genus *Neocorbicula* Fischer, 1887, species of which were formerly attributed to *Corbicula* Megerle, 1811 (e.g. Prime, 1865; Marshall, 1924, 1927). Parodiz and Hennings (1965) elevated the rank and clarified the taxonomy of the genus *Neocorbicula*, earlier proposed as a section or subgenus of *Corbicula*, and stated that South American taxa are referable to *Neocorbicula*.

Species of the genus *Corbicula* may have been introduced into the Río de La Plata basin between 1965 and 1975. Specimens belonging to this genus were first collected from the sandy banks at Punta Lara in February 1979 (Ituarte, 1981). In June 1978, *Corbicula* was collected from the Jacuí and Guaiba basins (Rio Grande do Sul, Brazil), with the species identified by Veitenheimer-Mendes (1981) as *Corbicula manilensis* (Philippi, 1844). According to Morton (1979), this species is a synonym of *C. fluminea* (Müller, 1774). Ituarte (1982) first reported *C. largillierti* (Philippi, 1844) at Colonia (Uruguay), on the eastern shore of the Río de La Plata.

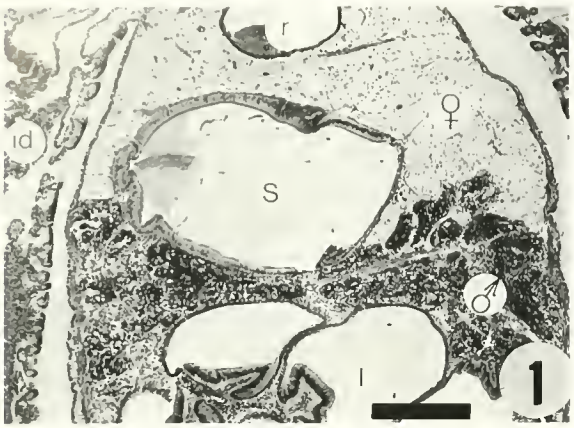
Veitenheimer-Mendes and Olazarri (1983) provided additional records along the Uruguay River from Las Cañas (south of Fray Bentos) to Punta Gorda (Department of Colonia) and from the eastern shore of the Río de La Plata to Arroyo Cufré (Department of San José), extending the known range of the genus. However, the specimens collected in their survey were not identified precisely.

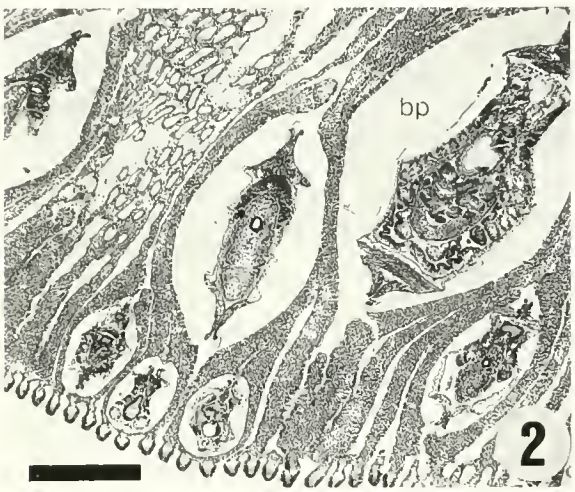
Ituarte (1984a) reported some biological aspects of a population of *C. largillierti* at Punta Lara, Río de La Plata. Ituarte (1985) described the growth dynamics in a natural population of *C. fluminea* at Punta Atalaya, Río de La Plata, extending its known range along the western shore of the estuary. In a brief communication, Olazarri (1986) suggested the presence of two Asiatic species of *Corbicula*, *C. largillierti* and *C. fluminea*, in the Uruguay Basin.

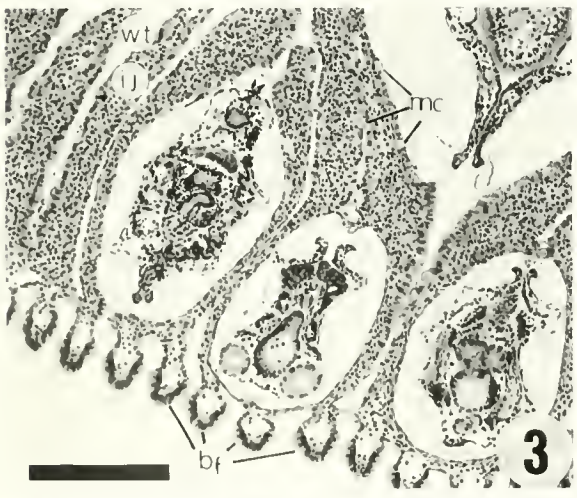
In the present paper, further data concerning the morphological characterization of the genera *Corbicula* and *Neocorbicula* are provided. The range of *Corbicula* species in Argentina has been extended to the Paraná River, and the species inhabiting the Uruguay River are identified. The distribution of the genus *Corbicula* along the Río de La Plata is reviewed and variation in shell shape due to environmental factors is discussed. Voucher specimens from this study are deposited in the invertebrate collections of the Museo de La Plata and Museo Argentino de Ciencias Naturales.

RESULTS

The Asiatic Clam genus *Corbicula* is represented in Argentinean and Uruguayan waters by two species, *C. fluminea* and *C. largillierti*. Present distribution of the genus in the Río de La Plata estuary (fig. 4) spans the entire western shore from the delta of the Paraná River to Magdalena City (35°02'S, 58°28'W) stretching approximately 75 km along the sandy intertidal zone. Bottom deposits are composed of fine sands and Paraná River sediments. Beyond Magdalena City, only isolated indi-







Figures 1–3. *Neocorbicula limosa*. **1.** Frontal section showing spatial segregation of male (ventral) and female (dorsal) tissues within the visceral mass. **2.** Sagital section of the inner demibranch showing embryos brooded within the water tubes. Cohorts of different ages are visible. **3.** Detail of figure 2, showing the advanced stage of development of embryos. All scale bars = 0.5 mm.

viduals of *Corbicula* were found. Darrigran (personal communication) collected both *C. fluminea* and *C. largillierti* at Punta Indio.

The distribution of *Corbicula* along the eastern shore of the Río de la Plata estuary is discontinuous. Veitenheimer and Olazarri (1983) had reported several records of *Corbicula* at San José and Colonia Departments without identification to species. The only fully identified record of Uruguayan *Corbicula* in the Río de la Plata River is a single lot of *C. largillierti* from Colonia (MACN 30175) identified by Ituarte (1982). Along the southern portions of the Río de la Plata estuary, *Corbicula* populations seem to have been limited by substratum characteristics (increased clay content) and a progressive increase in salinity caused by inflow of sea water during maximum high tides.

Three new records for both *C. fluminea* and *C. largillierti* from the upper course of the Paraná River are: Paso de La Patria, Isla Barranquera and Bella Vista (Province of Corrientes). Only *C. fluminea* was collected at San Nicolás, on the lower course of the Paraná River (Ituarte, 1982).

The Paraná River flows into the Río de La Plata estuary through a wide delta system, where both *C. fluminea* and *C. largillierti* have been collected. The former species seems to be more abundant in the Sarmiento River, the mouth of the Luján River, and the Arroyo Abra Vieja.

The genus *Corbicula* is present in the Uruguay River from Nueva Palmira to Fray Bentos. Both *C. fluminea* and *C. largillierti* were found in nearly all of the 41 samples taken in 12 transects of the river in this area. Veitenheimer-Mendes and Olazarri (1983) reported *Corbicula* from the following localities along the Uruguayan coast without identifying the species: Department of Colonia - Punta Gorda, Nueva Palmira; Department of Soriano - Agraciada, Concordia, Río San Salvador, Dolores; Department of Río Negro - Las Cañas Rivulet (southward to Fray Bentos). Of the many watercourses that flow into the Uruguay River from the Argentine shore, *C. largillierti* was found in only one, the Paranacito Rivulet. This species was also collected at Santo Tomé (Corrientes), the northernmost record from the Uruguay River.

Shell shape and especially shell outline are affected by such environmental factors as substrate composition, hydrodynamic forces, and other hydrological characteristics, including tidal regime. A typical trigonal shell outline, inflated beaks and uneroded umbos (extended into a rostrum posteriorly) are characteristic of individuals of

←

bf, branchial filament; bp, water tube expanded to form a brood pouch; e, embryo, ♀, female tissues, ♂, male tissues, f, intestine, id, inner demibranch; ij, interlamellar junction, mc, mucous cells, r, rectum, S, stomach, wt, water tube.

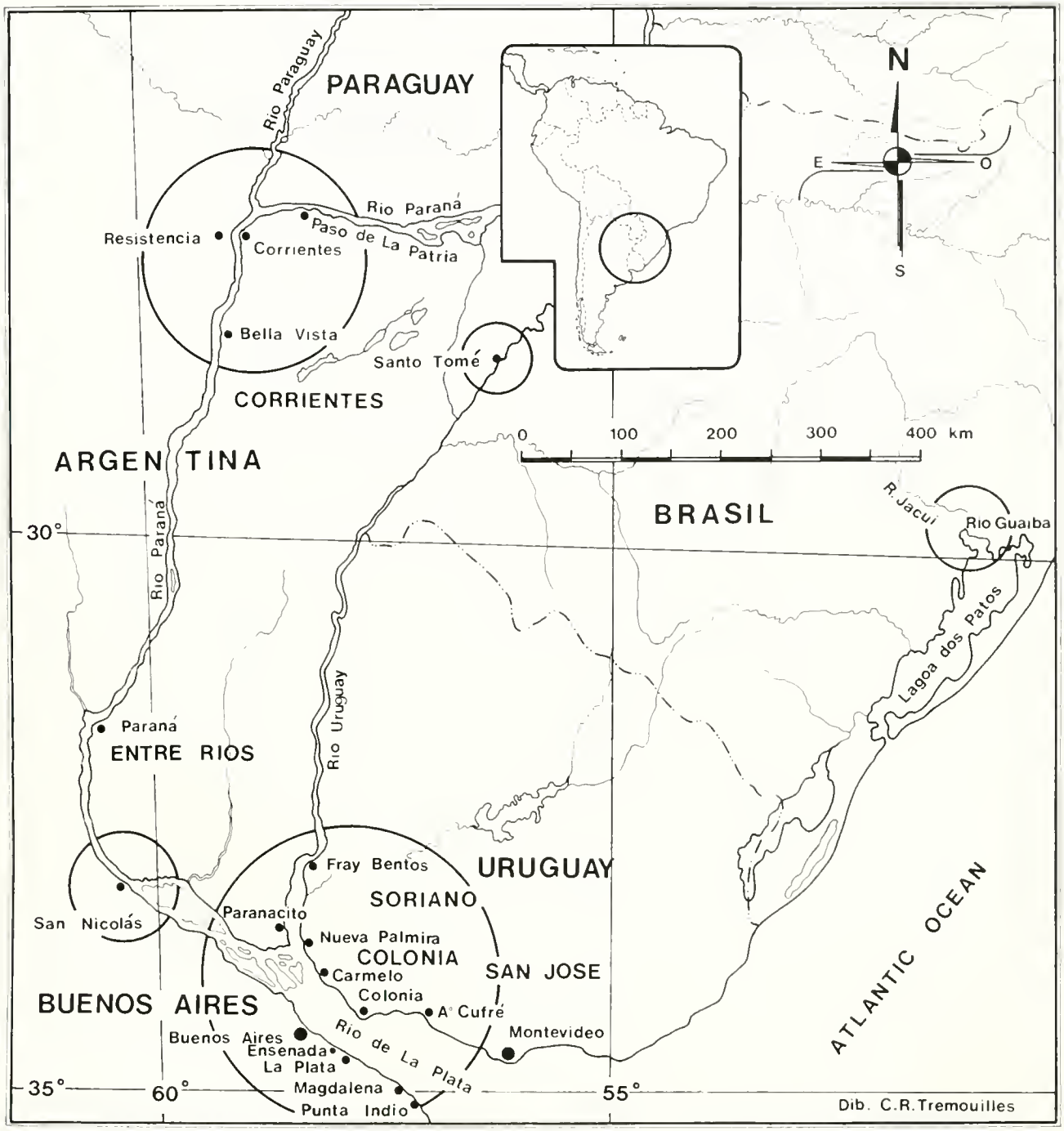
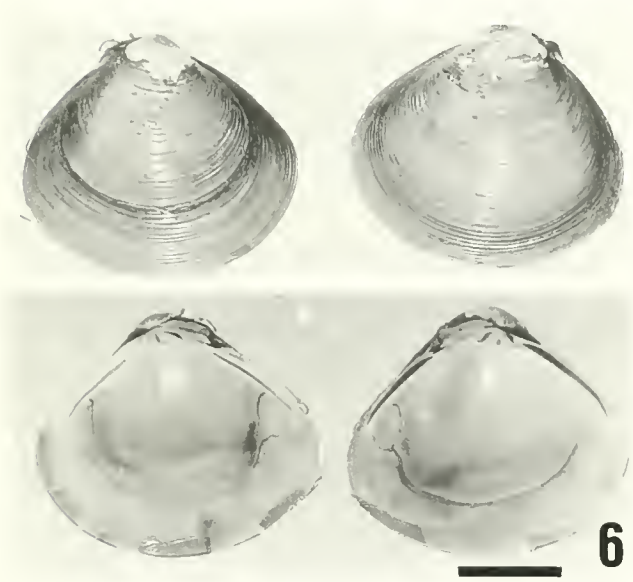
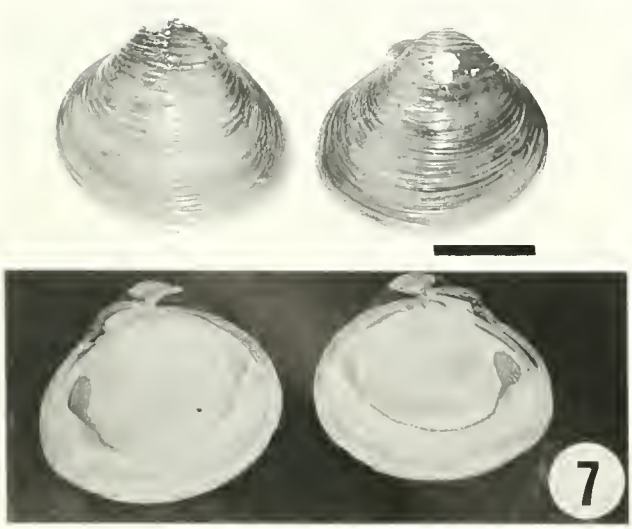


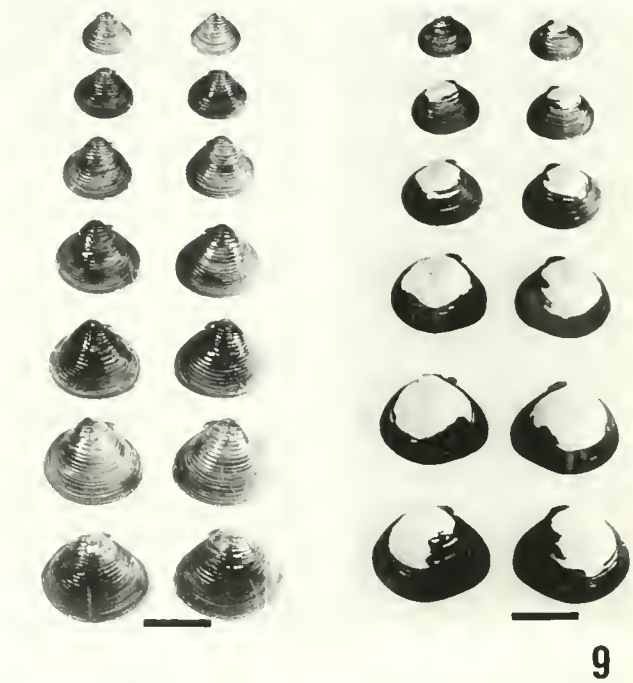
Figure 1. Distribution of *Corbicula* species in the southern Neotropical region, including new localities for *C. fluminea* and *C. largillierti*. See text for details.

C. fluminea that inhabit lentic and permanent environments with a soft substratum composed of mud or silt with variable sand content. Habitats composed of sand bottoms, with flowing water and or that are tidally affected contain specimens with a rounded or oval shell outline, and consequently higher Length/height (L/H) and length/width (L/W) ratios.

Examples of the effects of environmental factors on shell morphology can be found in the Río de La Plata at Olivos. Large populations of both *C. largillierti* and *C. fluminea* were present along the extended sand flat in the intertidal portion of the estuary. Hydrological conditions are strongly affected by the reduced slope in the intertidal. Tidal flows and waves increased in some cases by southeastern winds produced shells with oval outlines, eroded umbos and high values of L/H and L/







Figures 8–9. Series of specimens taken from tidal ponds (left) and sandy intertidal (right) habitats in Olivos, Buenos Aires, Río de La Plata. **8.** *Corbicula largillierti*. **9.** *Corbicula fluminea*. All scale bars = 10 mm.

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Figures 5–7. Corbiculids from Río de La Plata. **5.** *Neocorbicula limosa* (Maton, 1809) from the arroyo Miguelín. **6.** *Corbicula largillierti* (Philippi, 1844) from Punta Lara, Ensenada. **7.** *Corbicula fluminea* (Müller, 1774), from Olivos, Buenos Aires. All scale bars = 10 mm.

Table 1. Shell length/shell height (L/H) and shell length/shell width (L/W) ratios for *C. largillierti* and *C. flumínea* populations from different environments at Olivos, Río de La Plata ($\bar{x}$ = mean, S = standard deviation)

	C. largillierti					*C. flumínea*				
		L/H		L/W			L/H		L/W	
	n	$\bar{x}$	S	$\bar{x}$	S	n	$\bar{x}$	S	$\bar{x}$	S
Soft bottoms	101	1.13	0.02	1.56	0.05	52	1.17	0.04	1.77	0.05
Sandy intertidal	101	1.20	0.04	1.67	0.07	52	1.20	0.03	1.88	0.10

W (figs. 8,9; Table 1). Populations that settled in substrate depressions along the upper intertidal zone, which, like tide pools of the rocky marine intertidal areas, constitute small, lentic, micro-habitats with sand bottoms containing substantial amounts of mud or silt, have a typical trigonal shell outline, inflated beaks, thick shells, and lower L/W and L/H ratios. The posterior projection of the rostrum occurs only in *Corbicula flumínea* (Figs. 8,9, Table 1).

DISCUSSION

Parodiz and Hennings (1965) reported that the family Corbiculidae is represented in the southern neotropical region by the native genus *Neocorbicula* Fisher, 1887. In Argentina, *Neocorbicula limosa* (Maton, 1809) is found along the Uruguay and the Río de La Plata Rivers, while *N. paranaensis* (d'Orbigny, 1846) occurs in the Paraná River Basin. Although a considerable body of evidence has been presented to warrant the segregation of South American forms within the genus *Neocorbicula* (Parodiz & Hennings, 1965; Dall, 1902; Ituarte, 1984a, b, 1986) many authors persist in referring autochtonous taxa to the genus *Corbicula*. Conclusions based on this premise, including biogeographic (Counts, 1980; McMahon, 1983) and shell morphometric comparisons (Britton & Morton, 1979) are erroneous.

Corbicula and *Neocorbicula* differ substantially in shell morphology. The wide range of shell variability shown by both genera in response to environmental factors reveals that the most relevant character is the presence in *Neocorbicula* of a deeply marked pallial sinus (siphon lengths 12–14 mm). In *Corbicula* the pallial sinus is absent or represented by a slightly curved pallial line, and siphons as well as associated retractor muscles are scarcely developed (siphon lengths 3–4 mm) (figs. 5–7).

Branchial incubation of embryos, a characteristic common to both genera, is carried out in different ways. *Corbicula* incubate embryos in large numbers [> 10,000, as calculated for *C. largillierti* (Ituarte, 1984a)] within the water tubes of the two inner demibranchs. The basic structure of the inner demibranchs of *Corbicula* is unmodified, and differs from the outer demibranchs only in having fewer interlamellar junctions. *Neocorbicula*, on the other hand, develops brood pouches by cellular proliferation of the interlamellar junction epithelium of the inner demibranchs. Each brood pouch contains a single embryo. Gravid individuals usually have 20–30 brood pouches, and occasionally as many as 45 (Ituarte, 1984b) figs. 2,3). The incubation period of *Corbicula* is very short, with embryos released at a late veliger or pediveliger stage (200–240 μm diameter) (Ituarte, 1984a; Britton & Morton, 1979). In *Neocorbicula*, the incubation period is longer and the offspring are released as fully developed juveniles. Birth size in *Neocorbicula* is about 1.1 mm. However, some individuals from each cohort remain in the maternal gill until they reach 4–5 mm in shell length (Ituarte, 1984a) (figs. 2,3). In *Corbicula*, all embryos within a gravid individual show a similar degree of development, while in *Neocorbicula* two or three generations of larvae may coexist within each demibranch (Ituarte, 1984b) (fig. 2).

Those species of both genera that occur in the Americas are simultaneous hermaphrodites. However, there are differences in gonadal structure. During the early stages of gonadal development of *Neocorbicula* the predominant elements in the acinar wall are large and vacuolated follicular cells, with germ cells scattered along the base of the epithelium (Ituarte, 1986). In *Corbicula*, follicles are composed of minute follicular cells, with gonia the dominant elements in the acinar wall (Ituarte, 1984a). In *Corbicula* there is no pronounced segregation of male and female germinal cells within the gonad. If any degree of localization exists (Kraemer, 1978), it differs from that shown in *Neocorbicula*, where the ovary occupies the dorsal region of the gonad, while the testes develop in the ventral half (Ituarte, 1986) (fig. 1). Furthermore, in *Neocorbicula*, testes occupy more than 50% of the gonad (Ituarte, 1986) while in *Corbicula*, they occupy 15–30% (Kraemer & Lot, 1977; Britton & Morton, 1979).

Corbicula largillierti was described from the Yangtse-Kiang River in China, and its range includes northern and Central China as well as the Korean Peninsula (Prashad, 1929). The taxonomy of the Asiatic species of *Corbicula* was reviewed by Morton (1979), who reanalysed Prashad's (1929) "affinities" and regarded *C. largillierti* as belonging to a group of species that are synonymous with *C. flumínea* (Morton, 1979: Table 11). However, a re-examination of plots of affinities of Chinese, Korean and southeastern Russian species reveals *C. largillierti* to be distinct from any other species (Morton, 1979: Table 6). Moreover, there is no evidence in the text of Prashad (1929) to support the synonymy of *C. largillierti* with *C. flumínea*.

The material studied and assigned to *C. largillierti*,

which is now widely distributed in Argentinean waters, shows morphological differences from *C. fluminea* that are sufficient to to consider it a distinct species. *Corbicula largillierti* is characterized by its moderately thick shell, with fine, closely spaced concentric ridges and yellowish or greenish surface. Its shell is trigonal, nearly equilateral, and not greatly inflated. Its beaks are moderately inflated, the posterior end slightly protruded and obtuse at the extremity, even in larger individuals (fig. 6). *Corbicula fluminea* differs from *C. largillierti* in having a more solid shell, with coarser, more widely spaced surface sulcations. Its shell is more inflated and globous, with prominent and inflated beaks. In *C. fluminea*, the posterior margin is markedly protruded to form a characteristic rostrum, especially in specimens larger than 15 mm (fig. 7).

In spite of the highly variable shell morphology that results from environmental factors, the differentiating features listed above do not become masked, and the two species are easily distinguished even when populations of both species coexist in the same habitat.

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Sea Slugs and their Relatives of Western Australia

by Fred E. Wells and Clayton W. Bryce. 1993. Western Australian Museum, Perth, viii + 184 pp., 227 figs., 1 map. Softcover, $30.00 U.S. ISBN 0-7309-5523-0.

The opisthobranch gastropods or "sea slugs" of Western Australia have been gloriously introduced in this new book, a well-matched companion volume to *Seashells of Western Australia* by the same authors (Western Australian Museum, 1986) which treated only 16 species of opisthobranchs. Produced in virtually the same size and organization as the *Seashells* volume, it is also based on the collections and research activities of the Western Australian Museum in Perth, undoubtedly including the results of a series of international workshops, the last held in Albany in 1988. The authors extend this work as a sample rather than a complete coverage of this diverse fauna, but it's a substantial snack, at any rate, of 224 species in 42 families and 6 orders (Cephalaspidea, Thecosomata, Anaspidea, Notaspidea, Sacoglossa, and 147 species of Nudibranchia). All but a few are beautifully illustrated as living, crawling creatures in full (sometimes gaudy) color; only a few bubbles and pteropods are presented as empty shells.

Each higher taxon is briefly diagnosed and most are accompanied by a useful list of references from the primary literature (all but a few from the 1960's or later). Species descriptions include size, rarity, common synonyms, and overall geographical range plus specific occurrences in Western Australia. Again matching the *Seashells* volume, the geographical scope of this book includes the entire coastline of the state of Western Australia, from the tropical Kimberly region to the temperate Recherche Archipelago. The authors planned to (and in fact do) include representatives of each of the six orders from each of the three major zoogeographical regions, with over 40 cited localities. Added to this volume are records from late-1980's collecting on Christmas Island and the Cocos (Keeling) Islands, Australian Territories in the Indian Ocean. Although rather out-of-place, these 18 species records (7 of which are not found in Western Australia) do not seriously detract from the unity of this volume. Nevertheless, they might have been more effectively presented as a separate primary publication.

Both the pages preceding and following the main taxonomic section reflect those presented by the *Seashells* volume, with appropriate modifications and updated information. The introduction covers various aspects of opisthobranch biology (behavior, feeding, life histories), and the chapter on zoogeography has been expanded. Chapters on collecting and cleaning methods, covered fully in the *Seashells* volume, are understandably absent, in deference to Australia's recent collecting restrictions as well as opisthobranchs' rare standing in the average shell collection. Nothing is mentioned, however, on How to Photograph Sea Slugs, which would have been enormously welcome, since the photographs of living animals (many in obviously underwater surroundings) are the highlight of this book. A list of Western Australian shell clubs, a brief glossary (but not nicely illustrated as in the *Seashells* volume), and taxonomic index conclude the volume.

By this book, the authors have sought to "stimulate interest" and "demonstate both what is known, and also what is not known" about Western Australian opisthobranchs. They have succeeded on both counts through their recognition of ongoing research and of the unresolved taxonomic problems in this group. Forty-five species are identified to genus-level only (or with a tentative species assignment), with some noted as new to science (although, appropriately, none are originally described in this book). Over half are stated as rare or uncommon; many species are recorded from single localities. Ten species were described in the 1980's, another 10 in the 1990's (4 in 1993), as credit to the research efforts of a number of active opisthobranch biologists. One photograph of a living holotype (*Chromodoris aurigera* Rudman, 1990) is included. I cannot detect any glaring identification errors (although the spelling of Aplustridae is incorrect), and I happily note that the overall systematic treatment is up-to-date (perhaps due in part to a "who's who" list of contributors): *Akera* is placed in Anaspidea, *Cylindrobulla* in Sacoglossa, and *Aplustrum amplustre* in *Hydatina*, three recent changes often overlooked by non-specialists. Some might contest the wording of a few evolutionary statements (e.g., "elysiids have lost their shell"), but I think these are excusable in this context.

Wells and Bryce have elegantly met their intended goal to illustrate the extraordinary diversity of living opisthobranchs from the long, winding coastline of Western Australia. Attendees at future Western Australian Workshops (the next one in the Houtman Abrolhos in 1994) have a excellent guide to follow.

Paula M. Mikkelsen

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